

Middle-American Poeciliid Fishes of the Genera *Carlhubbsia* and *Phallichthys*, with Descriptions of Two New Species^{1, 2}

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(Plates I-VI; Text-figures 1-10; Maps 1 & 2)

TABLE OF CONTENTS

Introduction	1
Materials and Methods.....	2
Systematic Account	3
Genus <i>Carlhubbsia</i> Whitley.....	3
<i>Carlhubbsia stuarti</i> , new species.....	5
<i>Carlhubbsia kidderi</i> (Hubbs).....	8
Genus <i>Phallichthys</i> Hubbs.....	16
<i>Phallichthys amates</i> (Miller).....	18
<i>P. amates pittieri</i> (Meek).....	19
<i>P. amates amates</i> (Miller).....	22
<i>Phallichthys fairweatheri</i> , new species.....	24
Assessment of Taxonomic Criteria.....	29
Gonopodium	29
Gonopodial Suspensorium	30
Head Skeleton and Dentition.....	32
Sensory Canals	32
Relationships of <i>Phallichthys</i> and Status of the Poeciliopsinae	33
<i>Carlhubbsia</i> and the Cuban Endemic Poeciliids.....	35
<i>Girardinus</i> and <i>Quintana</i>	36
Characters Indicating Relationship of <i>Carl-</i> <i>hubbsia</i> with <i>Quintana</i> and <i>Girardinus</i>	36
Résumé of Morphological Analysis and Con- clusions	37
Zoogeographic Considerations	39
Summary	40
Acknowledgments	41
Literature Cited	41

INTRODUCTION

THE fishes of the family Poeciliidae (Order Cyprinodontiformes, also known as Cyprinodontida, Cyprinodontes and Microcyprini) are all from the New World and most of the species bear living young. They abound in the fresh and brackish waters of Mexico, the West Indies and northern and eastern South America, but attain their maximum diversity in Central America (Rosen & Gordon, 1953: 1-6). In Middle America three nominal species classified in two genera, *Carlhubbsia* (formerly *Allophallus*) and *Phallichthys*, have heretofore been regarded as closely related. Their many superficial resemblances include the asymmetric twisting or folding, either sinistrally or dextrally, of the external genitalium (gonopodium) of the adult male. This modification is shared by several other genera (*Poeciliopsis*, *Aulophallus*, *Phalloptychus* and *Xenophallus*). On the basis of this one feature, all of them have been grouped as the subfamily Poeciliopsinae (Hubbs, 1926; 1936).

We now find evidence, however, that asymmetry of the gonopodium is not in itself an adequate criterion of the implied phylogenetic relationships of the fishes in the Poeciliopsinae. As in other poeciliids, it is the fine details of the

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gonopodia and characters in the gonopodial suspensoria that provide the most useful criteria in determining relationship. On the basis of new data, *Carlhubbsia* shows affinities to *Quintana* and *Girardinus* (including *Toxus*, *Glaridichthys*, *Allodontium* and *Dactylophallus*); these are endemic Cuban fishes with symmetrical gonopodia. *Phallichthys* is closely allied to *Poeciliopsis* (including *Poecilistes*) and *Aulophallus*, but the remaining genera previously associated with them in the Poeciliopsinae are not intimately related. For these reasons the dissolution of the Poeciliopsinae is now recommended.

MATERIALS AND METHODS

Material.—Most of the specimens used in this study are preserved in the Museum of Zoology of the University of Michigan (UMMZ). Additional specimens are from the collections of the Chicago Natural History Museum (CNHM), Genetics Laboratory of the New York Zoological Society (NYZS-GAF) and the United States National Museum (USNM). In addition to most of the material of *Carlhubbsia* and *Phallichthys* previously recorded, we have had access to numerous and extensive series of the four known species belonging to these genera from Guatemala and Honduras. These were collected largely by the Rev. Gerald Fairweather, Drs. Myron Gordon, Carl L. Hubbs, Laurence C. Stuart and their field associates.

Counts and Measurements.—The methods of counting and measuring are those described by Miller (1948: 8-14) for certain cyprinodontid fishes. *Fin ray counts* include small anterior rays, but in dorsal and anal fins the last ray as counted consists of two elements that are separate to their bases. In the genera studied either one or two anterior dorsal rays are simple, the rest are branched distally. Careful examination under transmitted light is necessary to establish the number of simple rays, and since branching may be delayed, the definitive presence of a single simple ray can be reliably determined only in adults. *Caudal ray counts* include branched rays plus two. *Scales in lateral series* are counted from the upper angle of the gill aperture to the caudal base at midside. *Body-circumference scales* are counted from about two scale rows before the dorsal origin to an equal distance in front of the pelvic fins. The *vertebral count* includes the urostyle vertebral. *Head angle* is measured with an arm protractor: one arm is placed parallel to the predorsal contour (if flat) or tangential to it (if gently curved); the other is adjusted to coincide with the straight line along the lower surface of the head and the anterior part of the breast (the oblique upward slant of the lower

jaw is disregarded). *Standard length* is measured from snout tip to caudal base. *Head length* is taken to the opercular margin. *Diameter of orbit* is established by slipping caliper points within the orbital rim and spreading them gently. All measurements were recorded to tenths of millimeters.

Skeletal Material.—For clearing and staining, alcoholic (ethyl alcohol) specimens were washed briefly in tap water and transferred to 3% solution of KOH in tap water. Ten fish averaging 1½ inches in standard length were placed in 300 cc. of this macerating solution. When the fish became translucent in alkali (4 to 6 weeks at room temperature) enough Alizarin Red S was added to color the solution deep wine red. Within a week the bone and scales became intensely stained, and then all scales were removed. The fish were then placed directly into 50 cc. of glycerine where they cleared in about three days.

In disarticulating a skeleton for study a section of the cleared and stained specimen was first placed in warm 50% KOH solution. The rapid progress of the maceration was watched with a dissecting microscope; when minute bubbles formed, muscle and connective tissues were freed readily from the bone with a dissecting needle. As the bones separated they were transferred to cool tap water to which a few drops of acetic acid had been added to check further disarticulation.

Skeletons or parts thereof were drawn with the aid of a camera lucida. The material (in water or glycerine) was placed in a petri dish and intense reflected light was directed on it from illuminators on each side of the microscope stage. A manipulator fitted with solid glass needles was used to orient specimens. The camera lucida was adjusted to give a distortion-free image on the recording surface by sighting down a hollow tube placed at the geometrical center of the proposed drawing. The specimen was brought into line with the image of the hollow tube that was resting on the recording surface. Relative positions and dimensions of different structures were determined by utilizing the coordinate system of the graph paper employed as a drawing surface.

Preliminary drawings were refined and details added in free-hand from direct observations. The few cleared and stained skeletons were checked for accuracy by comparison with X-rays of series of specimens which were prepared as outlined by Miller (1957).

The distal part of the gonopodium is equipped with a variety of spine-like processes and other

specializations. The terminology here adopted for these structures is that proposed and described by Rosen & Gordon (1953: 18-23). For example, *spines* are specialized bony structures that arise on the ventral (anterior) surface of the distal third of ray 3; *serrae*, if present, are located on the posterior edges of rays 4 or 5, those found proximally on ray 4p function as an anchor for the collagenous tissue sheets that envelop the rays, those found near the distal end of the rays serve as holdfast structures during copulation; the *hook* is a terminal bony segment on ray 3 or ray 4a.

SYSTEMATIC ACCOUNT

GENUS *Carlhubbsia* WHITLEY

Allophallus.—Hubbs, 1936: 232 (original description; type species *Allophallus kidderi* Hubbs).

Carlhubbsia.—Whitley, 1951: 67 (replacement synonym of *Allophallus* Hubbs, which name is preoccupied by *Allophallus* Dziedzicki, 1923, in Diptera).

Description.—*Body* moderately deep and compressed, with distinctly or moderately angulated dorsal and ventral margins, covered with large cycloid scales. *Dorsal fin* typically falcate, often pointed, with 8 to 10, usually 9, rays; the first two rays simple (rarely only the first), other rays bifurcate one or more times (in adult). *Pelvic fin* without fleshy appendages, constantly with 6 rays, the second and third barely prolonged in adult males. *Anal* rays 9 to 11, usually 10. *Gonopodium* permanently folded to form a broad groove on the right side; single series of flat, irregular unpaired serrae on right half of ray 5p extending 8 to 20 segments beyond tip of ray 6; single series of unpaired serrae distally on the lateral margin of left half of ray 5a; single series of unpaired serrae originating distally on left half of ray 4p, tightly grouped into a cluster; distal and subdistal elements of ray 4p that lack serrae extremely slender, reduced or obsolescent; terminal segments of ray 4a widened transversely; ray 3 terminated by minute bony or membranous hook, without consolidated terminal or subterminal segments, right half of ray with row of unpaired broad and flat spines forming ventral wall of groove, left half with minute denticles on subdistal elements; segments of distal half of ray 6 swollen, transversely thickened, those of basal half asymmetrical, the paired elements not side by side; rays 7 and 8 simple, distinctly separated, not converging or in contact along middle of their lengths. *Gonopodial suspensorium* with three gonapophyses; uncini on first two gonapophyses emerging near base of

spine, not curved, moderately slender; uncini on third gonapophysis, if present, emerging midway along spine, usually closer to vertebral axis than tip of spine, not curved downward, moderately thickened, rarely slender; uncini of all gonapophyses overlapping one another, forming uncinar plane extending downward and backward at angle of approximately 30 to 45 degrees with horizontal. Dorsal half of primary gonactinostal complex greatly dilated antero-posteriorly, upper edge of complex slightly notched or uniform and unbroken. *Vertebrae* 28 or 29, rarely 30. *Pectoral girdle* somewhat triangular in outline, its longest dimension vertical; four discrete actinosts recessed within posterior margins of scapula and coracoid, not approximating lower margin of coracoid; upper part of cleithrum produced backward above scapula as large spatulate process; posterior edge of coracoid below actinosts produced backward as flat process similar in outline to cleithral process but smaller and variously developed. *Skull* deep and wedge-shaped, with well-developed supraoccipital processes and variously developed epiotic processes; jaws weak, consisting of slender elements with delicate articulations; preorbital (lacrymal) heavily sculptured, with a well-developed process extending backward toward lateral ethmoid; premaxillae and dentaries flattened in front, the paired elements not joined at midline and separated by a distinct tissue space, each with an outer series of movable, compressed or narrow incisor-like teeth in a single, largely transverse row that is weakly indented near midline, and an inner series of minute slender and pointed teeth in a narrow band from 1 to 3 teeth wide. *Intestine* long, coiled, lying largely on right side of coelom. *Peritoneum* dark. *Cephalic canals* rather well developed; supraorbital canal typically with a developed tube connecting pores 2, 3, and 4a, and a postorbital section connecting pores 6 and 7 (Gosline, 1949), sometimes with a third section connecting pores 4b and 5; preopercular canal typically with 7 pores; mandibular canal undeveloped; preorbital canal with 3 or 4 pores in adult. (See Table 1.)

Status.—*Carlhubbsia* consists of two distinct species, *C. kidderi* (Hubbs) and *C. stuarti*, n. sp. (pages 5-16, and Tables 1-5, 13-19), and probably a third, as yet undescribed because of inadequate material. The genus is confined to the Atlantic drainage of Middle America from the Isthmus of Tehuantepec to southern Guatemala.

Allophallus [= *Carlhubbsia*] *kidderi* was grouped by Hubbs (1936) with *Phallichthys amates* and *P. pittieri* in a subfamily Poeciliopsinae that Hubbs (1924) erected to include all

TABLE 1. COMPARISON OF TWO SPECIES OF *Carlhubbsia*
 Measurements are based on adults and are expressed as percent. of standard length

Character	<i>C. stuarti</i>	<i>C. kidderi</i>
Pectoral rays	13, rarely 14	9 or 10, rarely 11
Preorbital pores (adults)	Usually 4; if 3 with an open groove at ventral end	Usually 3; without groove
Vertebrae	Usually 28	Usually 29
Gonapophyses	With uncini on I and II only	With uncini on I, II and III
Gonopodium:		
Left half of ray 5a	With 15 to 20 terminal serrae	With about 6 terminal serrae
Left half of ray 5p	Continuous with terminal serrae on ray 5a	Obsolescent distally, not continuous with terminal serrae on ray 5a
Tip of ray 4p	With cluster of about 8 serrae	With cluster of 5 serrae
Body circumference scales	23 to 26; infrequently 23	22 to 24; infrequently 24
Dorsal fin	With dusky marginal band	With jet black spot near posterior margin
Vertical bars on body	Well defined	Faint
Dark scale borders	Not well marked	Well defined
Greatest body depth		
Males	39 to 42	27 to 30
Females	37 to 42	29 to 33
Least depth		
Males	22 to 25	14 to 18
Females	21 to 24	16 to 18
Predorsal length		
Males	54 to 58	50 to 54
Females	56 to 59	50 to 53
Preanal length		
Males	54 to 58	48 to 52
Females	64 to 67	57 to 62
Dorsal origin to caudal base		
Males	49 to 54	51 to 55
Females	48 to 51	50 to 54
Anal origin to caudal base		
Males	49 to 55	52 to 54
Females	40 to 42	42 to 45
Head length	29 to 34	25 to 30
Head width	18 to 20	14 to 18
Snout length	8 to 10	5 to 9
Postorbital length of head	11 to 13	9 to 12
Interorbital, bony width		
Males	13 to 15	9 to 10
Females	13 to 14	11 to 13
Dorsal fin, depressed length		
Males	31 to 34	27 to 32
Females	27 to 31	31 to 34
Anal fin, depressed length		
Males	36 to 41	49 to 54
Females	22 to 26	23 to 27
Size (standard length)		
Males	Usually 30-40 mm., largest 45 mm.	Usually 16-21 mm., largest 23 mm.
Females	Usually 35-50 mm., largest 55 mm.	Usually 25-40 mm., largest 51 mm.
Head angle	47° to 51°	37° to 42°

poeciliid genera in which the gonopodium of the adult male is asymmetrical. In his key to this group Hubbs (1936) utilized only the most general features of body form and tooth structure to associate *Carlhubbsia* and *Phallichthys*. He regarded the differences in their gonopodia as being sufficient for generic distinction.

Gonopodial Characters in Carlhubbsia.—The dextral folding of gonopodial rays 3, 4 and 5 in *Carlhubbsia* is accompanied by asymmetric modifications of many individual elements. Each type of segment ornamentation, e.g., spines, hooks and serrae (Rosen & Gordon, 1953), reflects the over-all asymmetry either by serial or unilateral reduction or by fusion and consolidation with adjacent or underlying structures. Thus, the basic architecture of the gonopodium in *Carlhubbsia*, as in other poeciliids with asymmetric gonopodia, is often masked by the superimposed concomitants of folding. In view of the proved value of specialized terminal features of the gonopodium to poeciliid taxonomy, it is of phylogenetic importance to distinguish between the basic pattern of terminal modifications and the asymmetric distortions to which the structure has been subjected.

Ray 3, for example, is bilaterally asymmetrical; the segments of the left half of this ray are simple oblong elements with minute denticles on the subdistal elements, whereas those of the right half are transversely widened with long, flat processes arising from their outer, ventral margins. The latter segments form a continuous ridge, that is, the ventral wall of the gonopodial groove. If this ridge is mechanically flattened, or viewed from above, the proximal section resembles the eccentric groove and the distal section the series of gonopodial spines that commonly occur in bilaterally symmetrical gonopodia in numerous poeciliid genera. The unilateral reduction of an entire series of segments and the distortion of the remaining series on ray 3 tends to obscure the character of the individual segment types. Nevertheless, these structures appear to have arisen in a manner similar to, if not identical with, the eccentric grooves and spines in forms with symmetrical gonopodia. For this reason they are so treated in our taxonomic reassessment.

Consequent to their reduction and consolidation in the evolution of asymmetrical gonopodia, some segments have become isolated from their parent rays and/or subsequently fused to others. The isolated cluster of serrae near the tip of the gonopodium in *Carlhubbsia* is known to arise from ray 4p because early developmental stages show these serrae to be continuous with the proximal elements of this ray. Subse-

quently the proximal elements are partly obliterated by fusion with the underlying segments of 4a.

The serrae on ray 5 in *Carlhubbsia kидderi* are isolated from the elements of 5p and are consolidated with the underlying segments of 5a; thus, in this species, they might appear as a *de novo* feature of ray 5a. In *C. stuarti*, however, these same serrae, though equally well consolidated with the segments of 5a, are continuous with the elements of 5p, which in this species are persistent. It seems certain, therefore, that these serrae in *Carlhubbsia* originated from a developmental field associated with ray 5p.

Carlhubbsia stuarti, n. sp.

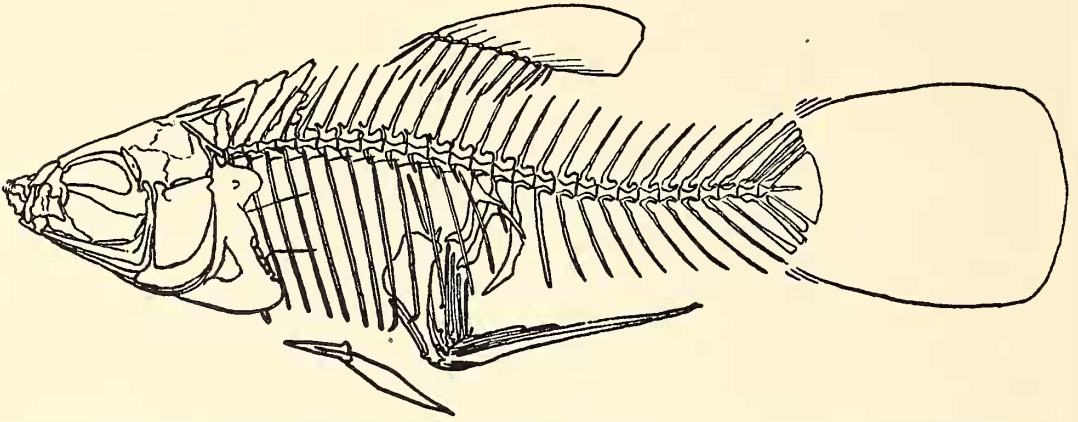
Pl. I; Text-figs. 1, 3, 5

Material.—The holotype (UMMZ 146084) is an adult male, 38.3 mm. in standard length, seined in the Río Polochic at the "playa," about 0.5 km. east of Panzós, Alta Vera Paz, Guatemala, on March 6, 1940, by Laurence C. Stuart. The allotype (UMMZ 172455), an adult female 50.5 mm. long, and 290 other specimens (UMMZ 146078) including half-grown and adult males and females from 29 to 55 mm. long, were taken with the holotype. UMMZ 146093, 5 subadult to adult specimens from 29 to 39.5 mm. long, seined in "El Canal," a diversion of Río Polochic, about 10 km. by river below Panzós, Alta Vera Paz, Guatemala, on March 8, 1940, by Stuart.

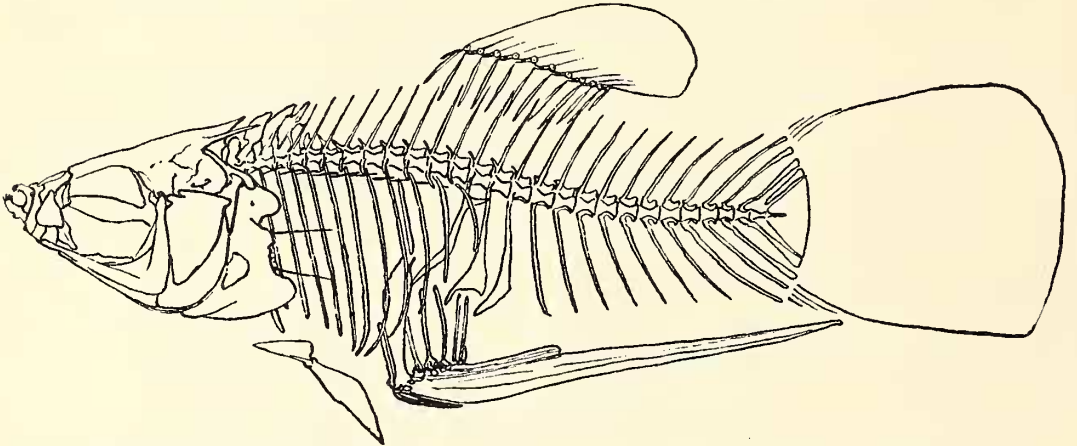
Diagnosis.—A large, deep-bodied, large-headed species of *Carlhubbsia* with 8 to 13 well to moderately developed narrow dusky bars on the side. Dorsal fin rather bluntly rounded anteriorly, projecting beyond succeeding rays to give the fin a falcate outline, with dusky distal band. Gonopodium with series of 15 to 20 terminal serrae on lateral margin of left half of ray 5a, the proximal members usually bidentate, the last member continuous with segments of ray 5p; tip of ray 4p with a cluster of approximately 8 serrae, the subdistal elements of this ray extremely weak but not obsolescent. Gonopodial suspensorium with uncini developed on gonapophyses I and II. Vertebrae 28. Preorbital canal with 4 pores in adult. Scales in lateral series 25 or 26. Body-circumference scales 23 to 26. Pectoral fin rays 13, rarely 14. Head angle 47° to 51°.

For the distinctive features of body and fin form, pigmentation and skeletal morphology, see also Tables 1-3, 13-18.

General Description.—A deep-bodied, robust species with moderately high and angular contours. In adult males the predorsal profile is



TEXT-FIG. 1. Skeleton of adult male *Carlhubbsia stuarti*, n. sp. Compare the following positional and structural features with these items in Text-fig. 2: (a) development of neural plates on anterior trunk vertebrae, (b) position of pelvic girdle, (c) curvature of distal tips of posterior pleural ribs, (d) form of first three sexually modified, attached hemal spines (gonapophyses), (e) relative positions of dorsal and anal fin origins, and (f) length of sexually modified anal fin (gonopodium). Tracing from an X-ray.



TEXT-FIG. 2. Skeleton of adult male *Phallichthys fairweatheri*, n. sp. See caption of Text-fig. 1. Tracing from an X-ray.

flat or slightly arched from nape backward and rises sharply to the dorsal origin; the dorsal and ventral margins of the caudal peduncle also are quite straight but taper rather gradually to the caudal base. In adult females the dorsal profile usually is slightly arched, and rises less abruptly to the dorsal origin; the anterior part of the caudal peduncle is relatively heavier in adult females and its slightly concave dorsal and ventral margins taper more abruptly to the caudal base. In both sexes the head angle measures 47° to 51° . In both sexes the snout is distinctly blunt and the lower jaw rises sharply and obliquely upward instead of outward from its articulation. The male is relatively deeper bodied than the female, and has more angular contours.

The dorsal fin is distinctly falcate in both sexes. The anal fin is broad and fan-shaped. In adult females the dorsal originates closer to caudal base than to snout, and the anal originates slightly behind the vertical from the dorsal origin. In adult males the two fins originate in the same plane as a result of the forward migration of the anal fin during sexual differentiation. The tip of the gonopodium extends posteriorly approximately two-thirds the distance from anal origin to caudal base. In both sexes the caudal fin is broad, subtruncate and only slightly rounded at its dorsal and ventral trailing edges, and is yellow toward the base. There are from 17 to 19 principal caudal rays, most often 17. The pelvic fins are well developed in both sexes

and are bright yellow. In adult females the pelvics are almost as long as the anal, originating on the belly one-half the distance from the anal origin to the edge of the opercle. When folded back the tip of the longest pelvic ray extends to the anal opening or barely overlaps the anal fin origin. In adult males the pelvics originate just anterior to the base of the gonopodium and the longest ray overlaps and extends beyond the bases of modified anal rays 1 and 2. In both sexes the pectoral fins are broadly spatulate and originate well below the midlateral line just behind the opercular margin; they extend obliquely upward and backward to a vertical from the dorsal origin.

The gillrakers on the outer face of the first arch, though well developed, are short and slender; they number 18 to 21.

Two principal pigment patterns on the trunk and caudal peduncle consist of a cross-hatched reticulum, most evident on the dorsum but clearly defined on the sides and venter as well, and a series of as many as 13 to 15 vertical bars superimposed on the reticular network. These bars are most pronounced in adult males. The bars are best developed on the caudal peduncle but extend anteriorly almost to the pectoral base. Each bar is long and slender, extending usually to within one scale row from the middorsal and midventral lines. There is no dark subocular bar or tear drop. In adults of both sexes the distal third of the dorsal fin is dusky. There is a basal band consisting of darkened interradiial membranes in the proximal third of the dorsal fin. Between the darkened bands, the middle third of the fin is lighter; anteriorly there is a light sprinkling of melanophores but posteriorly the membranes are clear. Probably this area was colored in life. Other fins are clear, with only a scattering of fine melanophores at their bases.

Skeletal Morphology.—The vertebral axis consists of 28 elements in each of 23 specimens X-rayed, including the holotype. The column is divided approximately in half into a precaudal or trunk series and a caudal series, the division being determined by the first hemal spine. In adult females, the first hemal spine usually emerges from the 15th vertebra. In adult males, the first hemal spine or gonapophysis is on the 14th vertebra. The vertebral axis takes the form of a gentle sigmoid curve, the precaudal section arching upward, especially in large adults. The first cervical vertebra bears no rib, but a pleural rib is present on most of the remaining precaudal vertebrae. The first rib is long and slender and is loosely articulated with the posterodistal margin of the transverse process of the second vertebra; the rib lies against the medial surface

of the pectoral girdle. Near the distal end of the rib there lies a free stylet-shaped bone which is expanded proximally and slender distally. This was termed the postcleithrum by Woods & Inger (1957: 247). This bone is well separated from the cleithrum and there is no other bone in series with it. The first 9 or 10 pairs of ribs are long, after which they diminish in size. The last definitive pleural rib usually occurs on the 13th vertebra but a delicate rudimentary rib may occur on the 14th. Minute epipleurals are present on all but the last two or three pleural ribs. In adult males the last five or six ribs are sexually modified. The last three or four are relatively small, extremely slender, and are widely separated at their tips; the tips of the preceding two or three ribs are bent sharply forward toward the pelvic girdle but do not converge. In adult males parapophyses occur on the first and second caudal vertebrae though they are usually quite small and closely applied to the base of the modified hemal spines or gonapophyses. In adult females parapophyses occur on the first two or three caudals. The so-called parapophyses of the more posterior trunk vertebrae, and of the anterior caudals in other species, actually are serially homologous with the transverse processes of the cervical and postcervical elements.

The gonopodial suspensorium of adult males receives a contribution from the vertebral axis of four specialized hemal spines. The first, or ligastyle, is a long, slender rod that originates on the 13th vertebra and migrates forward so that its dorsal margin comes to lie directly beneath the centrum of the 10th vertebra. The remaining three hemal spines become specialized chiefly by the addition of bony substance to their distal and posterior surfaces and are referred to as gonapophyses. The first two incline forward. Gonapophysis III is either slightly arched forward or essentially vertical. Only gonapophyses I and II bear uncini, which emerge proximally on the spines close to the vertebral centrum; the uncini of the second spine, however, are slightly farther down the shaft and more robust.

The actinosts of the anal fin in the adult male also are specialized and are incorporated into the suspensorial system as the gonactinosts (for general orientation see Rosen & Gordon, 1953: 11-13, Text-figs. 14-16). The first is a short, heavy, blunt rod that inclines sharply forward. It articulates with fin rays 1 and 2. Gonactinosts 2, 3 and 4 are fused to form a single highly complex plate of bone, the primary gonactinostal complex, which supports fin rays 3, 4 and 5. The complex is greatly dilated antero-posteriorly, having a distinct rostral bulge just above the tip

of the first gonactinost. The posterior lateral wings that are produced symmetrically from eccentric positions along either side of the core of gonactinost 4 are rather well developed, particularly at the dorsal third of the complex where they flare broadly. Gonactinost 5 lies embedded in the trough formed by the lateral wings of the primary complex. Gonactinosts 6, 7, 8 and 9 are slender and rod-like; they are closely joined and their tips converge slightly. Actinost 10 of the anal fin becomes much reduced or obsolescent and is incorporated into the base of gonactinost 9 as a tiny sliver of bone. The gonactinosts are firmly anchored to the vertebral axis by means of the ligamentous tissues associated with the ligastyle and the gonapophyses. The primary gonactinostal complex is associated with the ventral margins of the ligastyle and gonapophysis I. The tip of gonapophysis II interdigitates with gonactinosts 7 and 8. The tip of gonapophysis III curves forward toward the base of the final gonactinost.

The gonopodium in the adult male consists of the produced and modified rays 3, 4 and 5 of the anal fin. Together these three rays are folded to form a broad groove along the right side of the gonopodium. When held at rest, i.e., pointed caudally, ray 3 forms the ventral border, ray 5 the dorsal border and ray 4 the lateral wall of the dextral groove. The paired halves of ray 3 are segmented to the tip of the fin and are never consolidated. On ray 3 there is a series of from 15 to 20 long spinous processes which are followed distally by 5 to 8 simple terminal segments. The spines are present on the right half of the ray only; they form the ventral margin of the dextral groove. The terminal elements of ray 4a are expanded dorso-ventrally, and their segmentation axes are at right angles to the long axis of the ray. The elements of ray 4p are extremely delicate terminally but are never obsolescent. Its sinistral branch terminates in a cluster of 7 or 8 subtriangular serrae which face outward, away from the gonopodial groove on the convex surface of the permanently folded fin. On ray 5p there is a single series of unpaired retrorse distal serrae; they originate on the sinistral portion of this ray and are fused with the underlying segments of 5a. The unpaired serrae are subtriangular, approximately 15 in number. Several of the proximal members of this series are bidentate. Proximally on 5p, just below the tip of ray 6, there is a series of 5 to 10 minute retrorse serrae. The elements of ray 5a are flattened dorso-ventrally but are otherwise simple; they extend to the tip of the fin. The tips of all the rays became slender distally but show no significant displacement from their original axes;

they are grouped rather tightly together and are never separated by distinct tissue spaces. The gonopodium as a whole has a distinctly acuminate profile and is terminated by a rigid, hook-like cap of tough membranous tissue.

Relationship.—This species is clearly referable to the genus *Carlhubbsia* on the basis of details in the gonopodium and gonopodial suspensorium (see Text-figs. 3 and 5 and discussion on pp. 29-32). It may be separated readily from the only other known species, *C. kidderi*, by the characters listed in the diagnoses and in Table 1. The two species are allopatric, being separated geographically by a linear distance of approximately 45 miles in drainages which empty on opposite sides of the Yucatan Peninsula (Map 1). The origin and relationship of the members of the genus *Carlhubbsia* are discussed below (pp. 35-39).

Habitat.—At the two known localities Dr. Stuart recorded the water as muddy, but not excessively so, the bottom as sandy mud, the current as moderate and as slow, the temperature as warm, and the depth of capture as up to 5 feet.

Range.—*Carlhubbsia stuarti* is recorded only from the drainage of Río Polochic, Guatemala (Map 1). Robert R. Miller, in 1946, found this species to be common also in Lake Izabal, the terminus of Río Polochic.

Etymology.—This species is named in honor of Dr. Laurence C. Stuart in recognition of his efforts in collecting this and many other species of freshwater fishes in Guatemala during the past quarter-century.

Carlhubbsia kidderi (Hubbs)

Pl. II; Text-figs. 3, 5

Allophallus kidderi.—Hubbs, 1936: 232-238 (original description; Río Champotón, Campeche, Mexico). Scrimshaw, 1944: 182 (superfetation). Scrimshaw, 1945: 234-237 (viviparity). Scrimshaw, 1946: 21-22 (egg size).

Aulophallus kidderi.—Scrimshaw, 1945: 239-241 (lapsus for *Allophallus*).

Carlhubbsia kidderi.—Whitley, 1951: 67 (replacement synonym for *Allophallus*). Rosen & Gordon, 1953: 2, 28 (mechanics of gonopodium; reference by generic name only).

Material.—*Río Champotón drainage* (Campeche, Mexico): UMMZ 102206 (71 hf.-gr., ad. males and females, 16 to 40 mm. standard length), Río Champotón, at Janateya, 7 leagues east of Champotón, July 9, 1932, E. P. Creaser and A. S. Pearse; UMMZ 102199 (holotype of

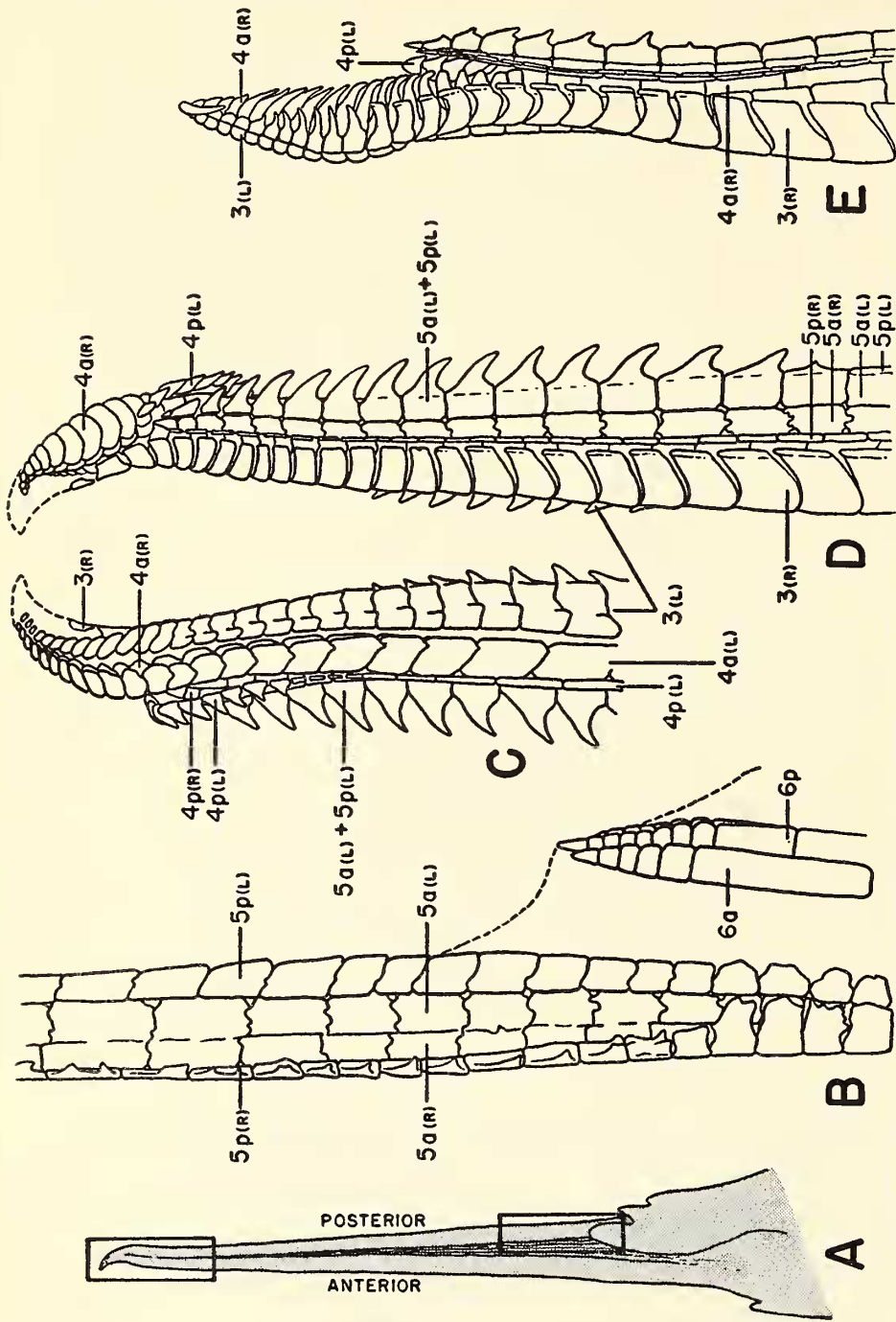


MAP 1. Lower Middle America giving distribution by record stations for the forms of *Carlhubbsia* and *Phallichthys*.

Allophallus kidderi Hubbs, 16 mm.) and UMMZ 102200 (3 subad., 11 to 16 mm.), Río Champotón, about 11 miles from mouth, July 11, 1932, E. P. Creaser.

Río San Pedro de Mártir drainage (El Petén, Guatemala): UMMZ 144206 (4 subad., 9 to 32 mm.), Laguna de Yalác, in course of Río San Pedro, about 6 leagues by river (easterly of El Paso de los Caballos), March 17, 1935, Carl L. Hubbs and Henry van der Schalie; UMMZ 144204 (185 hf.-gr., ad. males and females, 16 to 51 mm.), Laguna de Yalác, in course of Río San Pedro, about 6 leagues by river above El Paso de los Caballos, March 16, 17, 1935, Hubbs and van der Schalie; UMMZ 144205 (one ad. female, 39 mm.), Río San

Pedro, about ¼ mile below Laguna de Yalác, about 6 leagues by river east of El Paso de los Caballos, March 18, 1935, Hubbs and van der Schalie; UMMZ 144201 (28 hf.-gr. to ad., 17 to 42 mm.), north end of Laguna Perdida, 6 leagues south of El Paso de los Caballos, March 6, 7, 1935, Hubbs and van der Schalie; UMMZ 144202 (138 yg. to ad., 13 to 34 mm.), lagoon-like arm of Río San Pedro at El Paso de los Caballos, March 10-14, 1935, Hubbs and van der Schalie; UMMZ 144203 (94 hf.-gr. to ad. males and females, 16 to 35 mm.), lateral waters of Río San Pedro at Desempeño, just below El Paso de los Caballos, March 12, 1935, Hubbs; UMMZ 144207 (two ad. females 26 and 32 mm.), Río San Pedro, at Mactún Rapids, about

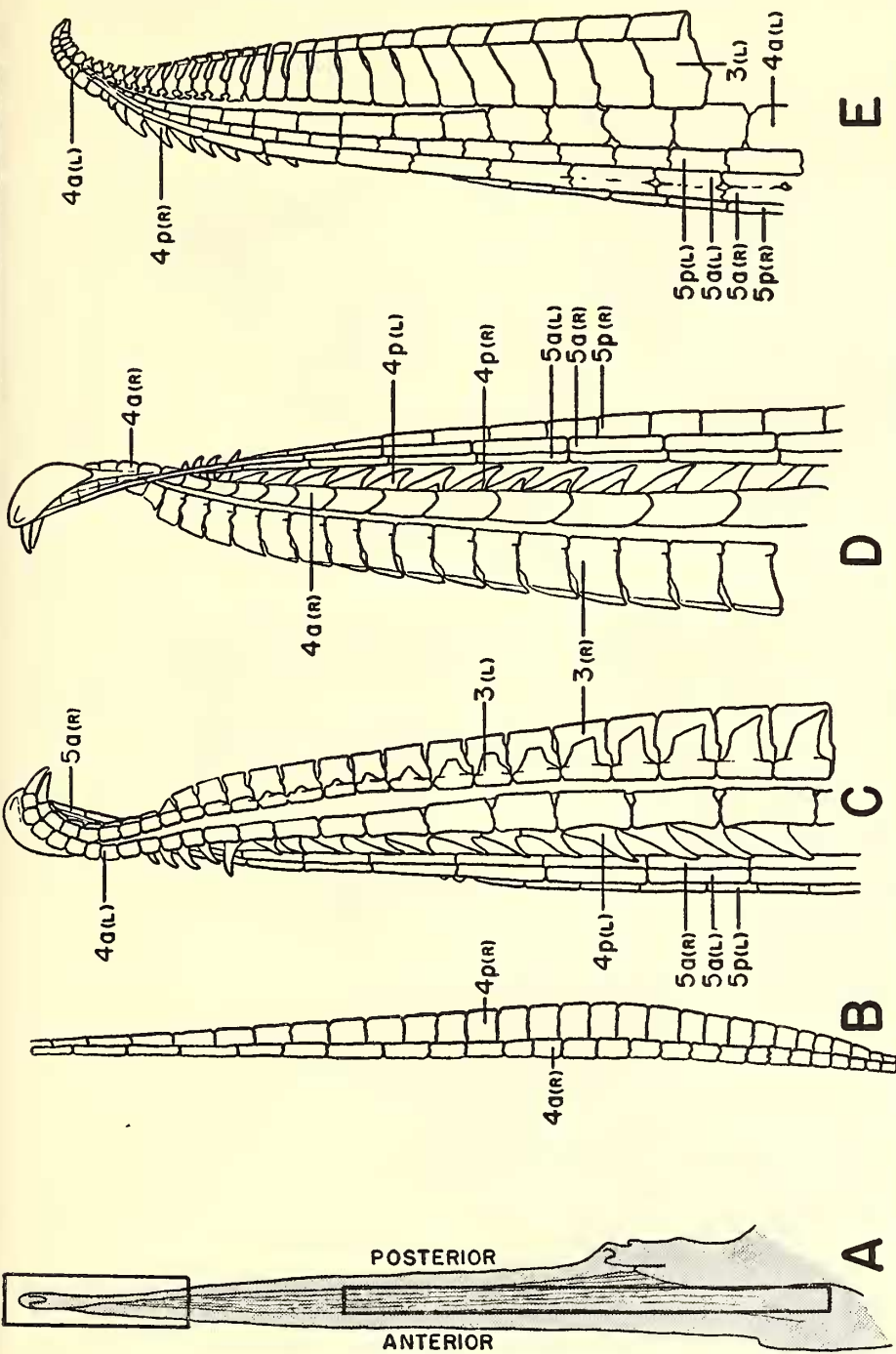


TEXT-FIG. 3. Details of gonopodia of the species of *Carluhubbia*. A. Gonopodium of *C. stuarti*, n. sp., as seen from the right side. The terms *posterior* and *anterior* refer to orientation of the unmodified rays of the anal fin of juveniles and females as they extend downward; with specialization of the anal fin as a gonopodium, the rays now extend backward directly underneath the male's body. Thus oriented, the originally posterior margin of each ray is dorsal and the anterior one ventral. (See also Text-fig. 1.) B. Proximal portions of rays 5 and 6 of the gonopodium of *C. stuarti*, n. sp., as seen from the right side. 5a (R) = right half of anterior branch of ray 5; 5p (L) = left half of posterior branch of ray 5; etc. This portion of the gonopodium is enclosed by the rectangle at the base of the fin in A. C. Distal tip of the gonopodium of *C. stuarti*, n. sp., as seen from a left three-quarter view to reveal marginal structures. D. Distal tip of the gonopodium of *C. stuarti*, n. sp., as seen from a right three-quarter view. This portion of the gonopodium is enclosed by the rectangle at the tip of the fin in A. E. Distal tip of the gonopodium of *C. kidderi* (Hubbs), as seen from a right three-quarter view.

60 miles by stream below El Paso de los Caballos (about two-thirds distance from Laguna de Yalac to Mexican border), March 20, 1935, van der Schalie.

Río de la Pasión drainage (Guatemala): UMMZ 144211 (5 ad. females, 27 to 31 mm.),

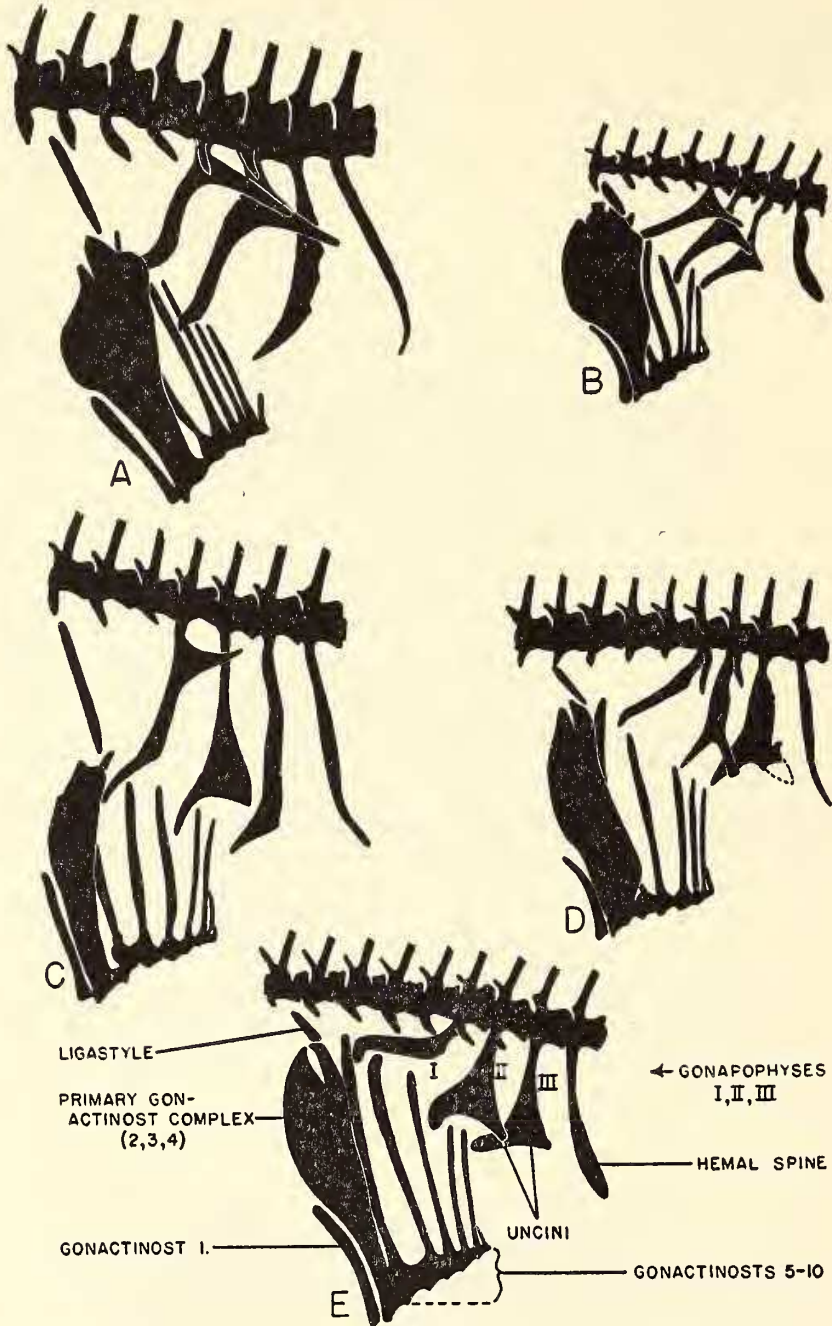
upper Río de la Pasión (=Río Chajmayic) at Ceiba (about 2½ miles by river below Seból), Alta Vera Paz, April 13, 1935, Hubbs; UMMZ 144212 (one ad. female, 41 mm.), mouth of first arroyo tributary to upper Río de la Pasión, from east below Arroyo San Simón, Alta Vera



TEXT-FIG. 4. Details of gonopodia of the forms of *Phallichthys*. A. Gonopodium of *P. fairweatheri*, n. sp., as seen from the right side. For terminology and orientation, see caption of Text-fig. 3. B. Proximal portion of ray 4 of the gonopodium of *P. fairweatheri*, n. sp., as seen from the right side, showing ridge-like unit formed from the high and laterally compressed segments of posterior branch. This portion of the gonopodium is enclosed by the rectangle at the base of the fin in A. C. Distal tip of the gonopodium of *P. fairweatheri*, n. sp., as seen from the left side, slightly unfolded longitudinally to reveal structural details. D. Distal tip of the gonopodium of *P. fairweatheri*, n. sp., as seen from the right side, slightly unfolded as in C. This portion of the gonopodium is enclosed by the rectangle at the tip of the fin in A. E. Distal tip of the gonopodium of *P. amates amates* (Miller), as seen from the left side.

Paz, April 16, 1935, Hubbs; UMMZ 144213 (157 yg. to ad. males and females, 6 to 40 mm.), flooded mouth of Arroyito Jolomax, opposite (south) El Cambio, El Petén, April 19, 1935, Hubbs; UMMZ 144214 (one ad. female, 25 mm.), Río de la Pasión, at Tres Islas, near

southern border of El Petén, April 20, 1935, Hubbs, van der Schalie and Taintor; UMMZ 144200 (103 hf.-gr. to ad. males and females, 9 to 32 mm.), Laguna de Eckibix (extreme west end), in savanna region southeast of Santa Ana, El Petén, February 26, 1935, Hubbs; UMMZ



TEXT-FIG. 5. Gonopodial suspensoria in the forms of *Carlhubbsia* and *Phallichthys*. For orientation, see Text-figs. 1 and 2. Parapophyses, which are not labelled, are small sinuous processes emerging near the bases of gonapophyses I and II in A, D, and E. A. *Carlhubbsia stuarti*, n. sp. B. *C. kidderi* (Hubbs). C. *Phallichthys fairweatheri*, n. sp. D. *P. amates amates* (Miller). E. *P. amates pittieri* (Meek).

144199 (14 hf.-gr. to ad. males and females, 11 to 27 mm.), Laguna de Eckibix (north shore), southeast of Santa Ana, El Petén, February 26, 1935, Hubbs; UMMZ 144198 (8 yg. to ad. males and females, 15 to 28 mm.), Laguna de Eckibix (south shore), southeast of Santa Ana, El Petén, February 26, 1935, Hubbs and van der Schalie; UMMZ 144215 (265 yg. to ad. males and females, 8 to 41 mm.), Arroyo San Martín, close to mouth into Río de la Pasión, east of Sayaxché, El Petén, April 22, 1935, Hubbs, van der Schalie, and Taintor; UMMZ 144216 (73 ad. females, 21 to 38 mm.), lowest mile of Arroyo de Petexbatúm, at and above Sayaxché, El Petén, April 23, 1935, Hubbs; UMMZ 144209 (26 hf.-gr. to ad. males and females, 14 to 35 mm.), Arroyo Subín, at Trinidad, about two miles east (above) Santa Teresa, south of La Libertád, El Petén, April 2, 1935, Hubbs and van der Schalie; UMMZ 144208, 144219, and 144210 (49 yg. to ad. females, 12 to 39 mm.), Arroyo Subín, Santa Teresa, about 13 miles south of La Libertád, El Petén, April 2-3, 1935, Hubbs, van der Schalie and Taintor; UMMZ 144218 (41 yg. to ad. males and females, 11 to 42 mm.), Arroyo Subín, tributary to Río de la Pasión in small bay connected with stream, beside third rapids (about 2½ miles from mouth), El Petén, April 25, 1935, Hubbs; UMMZ 144217 (127 yg. to ad. males and females, 12 to 39 mm.), Arroyo Subín, at second rapids (about two miles) above mouth into Río de la Pasión, El Petén, April 25, 1935, Hubbs.

Diagnosis.—A small, moderately deep-bodied, small-headed species of *Carlhubbsia* with 4 to 6 variably developed, narrow dusky bars on the side. Dorsal fin pointed, more or less falcate, with a conspicuous black blotch on the distal half of the posterior 3 or 4 rays. Gonopodium with series of approximately 6 terminal serrae on lateral margin of left half of ray 5a, left half of ray 5p becoming obsolescent 4 or 5 segments proximal to serrae; tip of ray 4p with cluster of 5 serrae, the subdistal elements of this ray extremely weak or obsolescent. Gonopodial suspensorium with uncini developed on gonapophyses I, II and III, those on III frequently weakly developed. Vertebrae usually 29, rarely 28 or 30. Preorbital canal with three pores in large specimens, or undeveloped and represented by an open groove in small males. Scales in lateral series 26 or 27. Body-circumference scales 22 to 24. Pectoral fin rays 9 to 11, usually 10. Head angle 37° to 42°.

The distinctive features of body form are presented in Tables 4 and 5, and the two known species of *Carlhubbsia* are contrasted in Table 1.

Range.—*Carlhubbsia kidderi* is known to oc-

cur in the Río Champotón, Campeche, Mexico, and in the drainages of Río San Pedro de Mártir, El Petén, Guatemala, and Río de la Pasión, Alta Vera Paz and El Petén, Guatemala (Maps 1 and 2). These latter rivers flow into the Río Usumacinta, and it is predictable that when this system is better explored ichthyologically the known range of *C. kidderi* will be substantially increased. During the Fifth Carnegie Institution-University of Michigan Expedition to El Petén, in 1935, Drs. Carl L. Hubbs and Henry van der Schalie failed to take this species in Laguna de Petén or other adjacent disjunct waters of the area, but did collect it in Laguna Perdida and Laguna de Eckibix (Map 2).

Habitat.—The environment where this species was found in El Petén by Drs. Carl L. Hubbs and Henry van der Schalie in 1935 indicates a broad variation in habitat tolerance. To judge by the conditions prevailing where especially large samples were obtained, however, *Carlhubbsia kidderi* prefers quiet to slow-moving water; a bottom composed of soft, flocculent silt, muck or soft mud, or organic litter, with or without some gravel or rocks; moderate to dense vegetation; and shallow shore areas or protected lagoons. At most stations the water was warm or hot and varied from clear to roily or turbid.

Remarks.—To the description of *Carlhubbsia kidderi* by Hubbs (1936: 234, items 5d and 6d of key), we make the following corrections and additions: In 5d, the first sentence reads “. . . rather compressed but pointed incisors, not forming an even cutting edge . . .” Since the teeth are pointed, not chisel-like, the cutting edge is in a sense irregular. However, the tips of the teeth form a straight rather than an irregular or zigzag cutting edge. Also, the teeth of the outer series in *kidderi* originate on the same dental margin and lie side by side, in strong contrast to the arrangement of this series in such species as *Girardinus metallicus* in which the teeth originate on a broad dental ridge, overlap one another shingle fashion, and form a complex cutting edge. In 6d, the sixth sentence ends “. . . segments of left side only [ray 5a], modified into flat serrae proximal to and partly opposite the serrae of ray 4.” This statement should be omitted and the following incorporated at the beginning of the seventh sentence: “Left half of ray 5p becoming obsolescent and merging with 5a at the level of the 12th to 18th segment (counting apico-basally on 5a) and reappearing on the 8th or 9th element of ray 5a as 5 or 6 flat serrae that are fused to the underlying segments; right half of ray 5p made up of delicate, almost thread-like segments, extending unbroken

TABLE 2. PROPORTIONAL MEASUREMENTS OF TEN ADULT MALES OF *Carlhubbsia stuarti*

Proportions are expressed in thousandths of the standard length.

See text for source of specimens.

Measurement	UMMZ 146078						Holotype UMMZ 146084	UMMZ 146078		
	45.3	44.1	41.1	38.7	38.5	38.5	38.3	38.2	37.6	34.0
Standard length (mm.)	45.3	44.1	41.1	38.7	38.5	38.5	38.3	38.2	37.6	34.0
Body, greatest depth	411	408	401	401	403	400	405	424	404	388
Caudal peduncle, least depth	232	238	231	235	231	231	248	233	226	218
Dorsal origin to snout tip	548	556	557	566	569	571	574	560	564	547
Anal origin to mandibular symphysis	545	553	564	576	558	564	574	571	572	573
Dorsal origin to caudal base	521	528	513	517	499	512	535	518	516	488
Anal origin to caudal base	550	522	511	509	525	512	522	531	513	491
Head length	300	306	292	310	301	299	313	314	317	312
Head width	188	197	187	194	195	187	188	194	200	188
Snout length	88	98	85	90	81	91	91	92	82	88
Orbit length	106	113	109	109	106	109	110	113	120	118
Postorbital length of head	115	120	122	127	119	122	117	118	128	118
Orbit to angle of preopercle	46	57	54	52	42	49	60	56	51	47
Interorbital, bony width	132	136	131	142	143	143	144	136	144	132
Mouth, over-all width	88	95	95	90	91	93	97	97	106	88
Dorsal fin, depressed length	311	318	326	318	317	311	339	340	319	312
Anal fin, depressed length	373	365	380	390	390	390	399	393	396	409
Caudal fin length	364	365	389	377	390	377	397	398	391	406
Pectoral fin length	269	268	292	287	273	278	292	288	290	294
Pelvic fin length	212	200	219	209	221	208	227	223	213	206

TABLE 3. PROPORTIONAL MEASUREMENTS OF TEN FEMALES OF *Carlhubbsia stuarti*

The smallest specimen is a juvenile; the others are adult. Proportions are expressed in thousandths of the standard length. See text for source of specimens.

Measurement	UMMZ 146078			Allotype UMMZ 172455	UMMZ 146078					
	51.8	51.5	50.6	50.5	49.5	45.3	44.3	39.1	38.5	31.4
Standard length (mm.)	51.8	51.5	50.6	50.5	49.5	45.3	44.3	39.1	38.5	31.4
Body, greatest depth	396	394	377	396	398	382	399	402	416	420
Caudal peduncle, least depth	224	214	217	220	222	221	219	223	223	236
Dorsal origin to snout tip	570	583	583	584	572	559	576	563	571	576
Anal origin to mandibular symphysis	657	656	646	669	642	654	652	665	665	669
Dorsal origin to caudal base	496	491	486	489	495	497	485	499	509	494
Anal origin to caudal base	413	414	421	408	404	408	420	420	410	398
Head length	294	291	292	297	291	298	305	312	312	338
Head width	183	184	192	178	182	185	187	192	200	194
Snout length	87	87	81	91	89	88	90	92	90	96
Orbit length	98	101	97	103	105	97	108	105	112	118
Postorbital length of head	118	115	119	119	113	117	115	128	127	143
Orbit to angle of preopercle	58	52	55	55	57	44	56	54	60	64
Interorbital, bony width	133	132	132	135	133	135	129	141	140	140
Mouth, over-all width	87	87	89	93	89	88	86	95	93	89
Dorsal fin, depressed length	276	276	294	287	283	287	282	299	301	309
Anal fin, depressed length	224	221	229	230	228	232	244	253	244	264
Caudal fin length	338	332	346	348	354	336	363	361	379	389
Pectoral fin length	251	252	257	261	248	252	262	263	262	274
Pelvic fin length	193	194	207	202	198	201	194	205	208	210

TABLE 4. PROPORTIONAL MEASUREMENTS OF TEN ADULT MALES OF *Carlhubbsia kidderi*
Proportions are expressed in thousandths of the standard length.
See text for source of specimens.

Measurement	UMMZ 144203									
	20.5	20.0	19.7	19.7	19.3	18.0	18.0	16.5	16.5	16.0
Standard length (mm.)	20.5	20.0	19.7	19.7	19.3	18.0	18.0	16.5	16.5	16.0
Body, greatest depth	288	295	299	299	295	289	289	273	273	275
Caudal peduncle, least depth	171	175	173	173	176	167	167	145	164	156
Dorsal origin to snout tip	512	515	528	503	503	528	506	533	527	525
Anal origin to mandibular symphysis	488	500	508	497	482	500	489	515	485	500
Dorsal origin to caudal base	522	525	523	513	518	528	533	515	515	550
Anal origin to caudal base	522	520	528	533	518	528	533	539	521	538
Head length	278	275	284	274	269	256	261	273	273	288
Head width	141	150	147	147	145	139	139	145	152	138
Snout length	68	75	76	66	62	56	56	61	73	56
Orbit length	107	105	107	102	104	100	106	103	103	100
Postorbital length of head	112	105	107	102	104	100	106	91	97	94
Orbit to angle of preopercle	49	55	66	51	52	56	56	42	42	50
Interorbital, bony width	93	90	91	91	93	94	94	91	91	94
Mouth, over-all width	83	90	86	86	78	83	89	79	85	81
Dorsal fin, depressed length	293	320	...	284	285	306	306	...	291	275
Anal fin, depressed length	488	540	528	533	518	528	528	533	533	525
Caudal fin length	350	...	337
Pectoral fin length
Pelvic fin length	195	210	203	203	202	194	194	182	200	188

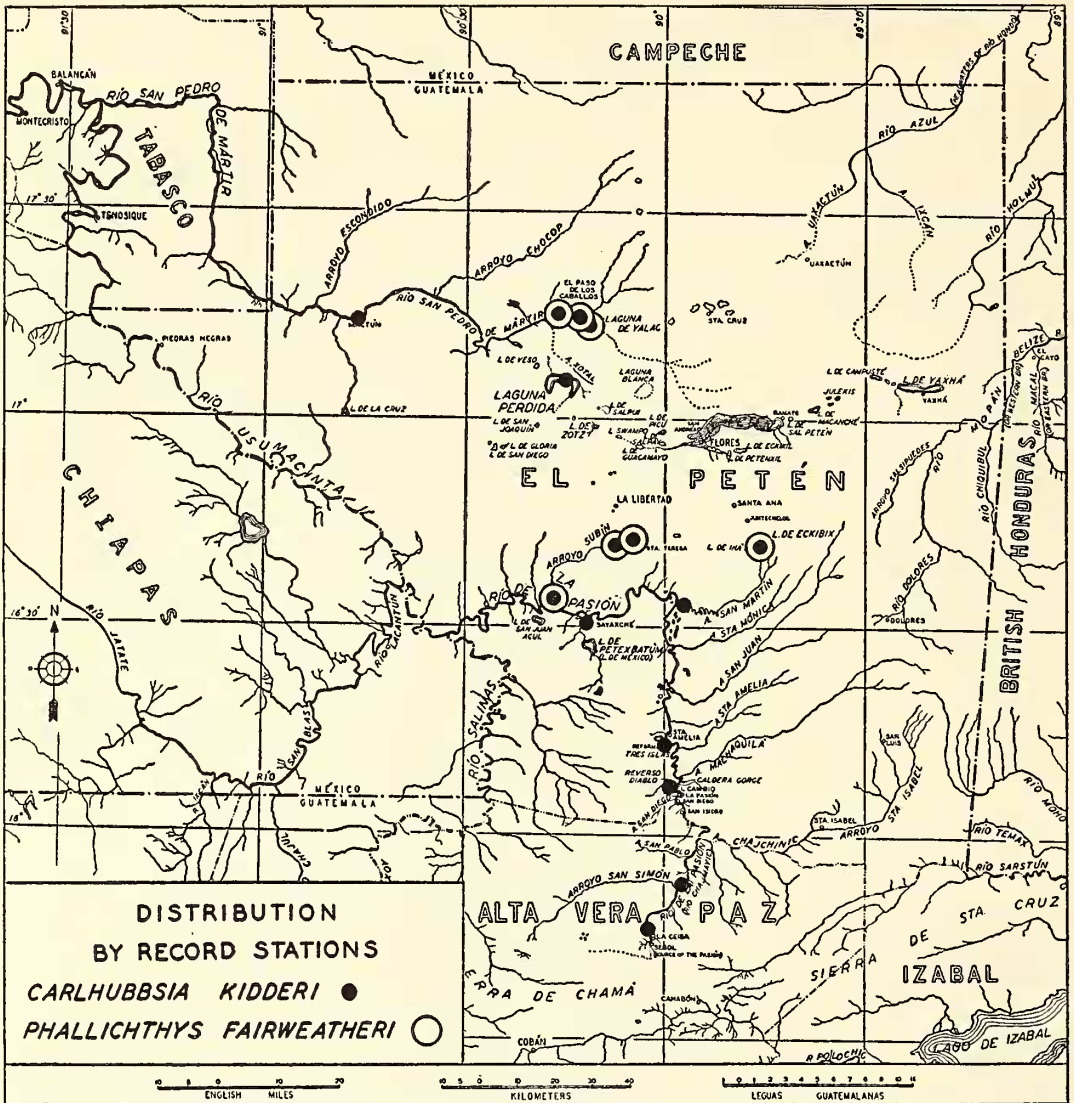
TABLE 5. PROPORTIONAL MEASUREMENTS OF TEN ADULT FEMALES OF *Carlhubbsia kidderi*
Proportions are expressed in thousandths of the standard length.
See text for source of specimens.

Measurement	UMMZ 144203									
	34.5	33.0	32.9	32.0	31.7	31.4	30.1	28.9	28.5	27.9
Standard length (mm.)	34.5	33.0	32.9	32.0	31.7	31.4	30.1	28.9	28.5	27.9
Body, greatest depth	319	321	304	309	322	296	312	308	326	315
Caudal peduncle, least depth	174	179	170	169	170	172	179	166	179	172
Dorsal origin to snout tip	522	512	508	513	514	513	518	519	519	523
Anal origin to mandibular symphysis	609	597	605	609	603	576	608	578	618	595
Dorsal origin to caudal base	516	518	538	516	521	513	508	522	502	527
Anal origin to caudal base	452	439	432	447	426	436	429	443	425	444
Head length	290	288	289	294	293	293	286	291	298	287
Head width	157	164	158	159	155	162	166	173	175	165
Snout length	84	82	85	84	85	86	80	87	88	82
Orbit length	107	112	109	109	110	118	113	111	119	108
Postorbital length of head	110	112	112	113	110	115	110	97	105	100
Orbit to angle of preopercle	52	55	52	56	54	51	56	48	56	50
Interorbital, bony width	113	118	116	119	117	115	116	114	123	111
Mouth, over-all width	90	91	88	81	91	89	86	87	91	86
Dorsal fin, depressed length	334	309	311
Anal fin, depressed length	258	...	243	233	270
Caudal fin length	256	349
Pectoral fin length	235	...	243	221
Pelvic fin length	194	182	198	191	192	188	196	194	193	190

to within 4 or 5 segments of the tip of ray 5a; ...” (See discussion on p. 5).

The following account of the pigmentary characters of living *Carlhubbsia kidderi* is taken from original notes made by Carl L. Hubbs in 1935 in El Petén, Guatemala. Coloration of

adult male: Dorsal fin [with] bright orange yellow. Caudal peduncle bright yellowish, becoming almost orange above anal fin. Trunk proper without yellow. Anal fin yellow; pelvic orange-yellow. Some males show a reduction in the amount of yellow pigment on body and



MAP 2. El Petén, Guatemala, and adjacent areas showing collection localities in Guatemala for *Carlhubbsia kidderi* and *Phallichthys fairweatheri*. The base map was compiled by Carl L. Hubbs and Henry van der Schalie in 1937.

fins. Coloration of adult female: Olive, with silvery luster on sides of belly; golden amber elsewhere. Dark bars weak, barely evident. Dorsal fin orange-amber, jet black toward posterior outer angle, dusky toward upper margin, bright clear yellow-amber just before black spot. Some orange amber on other fins, especially anal and pelvic.

GENUS *Phallichthys* HUBBS

Phallichthys.—Hubbs, 1924: 10 (type species, by original designation, *Poeciliopsis isthmensis* Regan, a subjective synonym of *Phallichthys amates pittieri* Meek).

Description.—Body deep, moderately compressed, with angulated dorsal and ventral margins, covered with large cycloid scales. Dorsal fin rounded, with 8 to 11 rays, the first one or two simple, the other rays bifurcate one or more times (in adult). Pelvic fin without fleshy appendages, constantly with 6 rays, the second and third somewhat prolonged in adult males. Anal rays 9 or 10. Gonopodium permanently folded to the right or left to form a broad groove; ray 5p modified as laterally compressed knife-like ridge forming dorsal wall of groove on left (in sinistral species) or right (in dextral species) half; ray 4p high, laterally compressed and ridge-

like proximally, with row of unpaired distal serrae on right (in sinistral species) or left (in dextral species) half, sometimes with 5 or 6 minute serrae on right half in dextral species; ray 3 with row of unpaired, broad, flat and moderately incurved spines forming ventral wall of groove on left (in sinistral species) or right (in dextral species) half, without consolidated terminal or subterminal segments; segments of distal half of ray 6 swollen, transversely thickened, those of basal half asymmetrical, the paired elements not side by side; rays 7 and 8 distinctly separated, not converging or in contact along middle of their lengths. *Gonopodial suspensorium* with three gonapophyses; uncini on first gonapophysis, if present, emerging near base of spine just below vertebral centrum; uncini of second and third gonapophyses always situated distally on spines to form broad swellings, the tips arching ventrally. Primary gonactinostal complex long, slender, narrow antero-posteriorly. *Vertebrae* usually 28 or 29, rarely 27 or 30. *Pectoral girdle* somewhat triangular in outline, its longest dimension vertical; four discrete actinosts recessed within posterior margins of scapula and coracoid, not approximating lower margin of coracoid; upper part of cleithrum produced backward above scapula as large spatulate process; posterior edge of coracoid below actinosts produced backward as flat process similar in outline to cleithral process but smaller. *Skull* deep and wedge-shaped, with well developed supraoccipital processes and variously developed epiotic processes; jaws weak, consisting of slender elements with delicate articulations; preorbital (lacrymal) little sculptured, subtriangular in outline; premaxillae and dentaries flattened in front, the paired elements not joined at midline and separated by a distinct tissue space, each with an outer series of movable, compressed or narrow incisor-like teeth in a single, largely transverse row that is weakly indented near midline, and an inner series of minute pointed teeth in a band of variable breadth. *Intestine* long, coiled, lying largely on right side of coelom. *Peritoneum* dark. *Cephalic canals* rather poorly developed; supraorbital canal variously incomplete, sometimes reduced to short, postorbital tube connecting pores 6 and 7 (Gosline, 1949), sometimes, especially in large adult females, with short section of tube above eye connecting pore 3 with pores 2 and/or 4a; preopercular canal typically with 7 pores; mandibular canal never developed; preorbital canal with 3 pores in adult, often with two pores and open groove in subadults.

Status.—*Phallichthys* has previously been associated closely with *Carlhubbsia* [as *Allophallus*]

(Hubbs, 1936). Despite strong superficial resemblance between these genera, we find compelling evidence, especially in the comparative morphology of the gonopodium and the gonopodial suspensorium, to regard *Carlhubbsia* as representative of a distinct phyletic line including also the Cuban endemic genera *Girardinus* and *Quintana*, whereas the relatives of *Phallichthys* are to be found in the *Poeciliopsis* complex. The common presence of a folded gonopodium in *Phallichthys* and *Carlhubbsia* is interpreted as the product of parallel evolution. As discussed hereinafter, the nominal subfamily Poeciliopsinae (Hubbs, 1924) based on this supposedly monophyletic feature is in need of re-evaluation.

Phallichthys includes three known allopatric forms which occur on the lowlands of the Atlantic slope of Middle America, ranging from western Panama to northern Guatemala and British Honduras. The distinctive northern species, *P. fairweatheri*, is sympatric with *Carlhubbsia kideri*. As in the species of *Carlhubbsia* the gonopodial groove in *P. fairweatheri* is dextral. The forms with sinistral gonopodia, *pittieri* from western Panama and Costa Rica and *amates* from northern Honduras and eastern Guatemala, are well separated geographically but are strikingly similar in general appearance and in most diagnostic characters (Henn, 1916; Hubbs, 1924 and 1926). These two are herein treated as subspecies of *P. amates*.

Both *Phallichthys amates* and *P. fairweatheri* have been maintained in the laboratory. As might be anticipated from their body form, they are not agile swimmers, and they progress by means of a series of short, hesitant dashes. In aquaria they are almost exclusively bottom feeders and are rather "timid." An effort was made to hybridize *P. fairweatheri* from British Honduras with a commercial stock of *P. amates*. Six pairings, *amates* ♂ × *fairweatheri* ♀, and four pairings, *fairweatheri* ♂ × *amates* ♀, were uniformly unsuccessful in producing offspring, although homotypic *amates* and *fairweatheri* matings set up at the same time did yield offspring. Each heterotypic pair was isolated in a five-gallon aquarium; the pairings were maintained for eight months (December to July) before being abandoned because of mortalities among the *P. fairweatheri*. Three of the direct and two of the reciprocal matings had been set up in a constant-temperature room with a controlled 12-hour light cycle. Whether or not *fairweatheri* and *amates* are fully isolated reproductively can only be determined by additional experimental matings under a wider variety of aquarium conditions. It is not known whether males of one species actually attempted to copulate with fe-

TABLE 6. COMPARISON OF THE SPECIES OF *Phallichthys*
Measurements are from adults and are expressed as percent of standard length

Character	<i>P. amates</i>	<i>P. fairweatheri</i>
Scales in lateral series on body	26 or 27	22 to 24
Anal fin rays	Usually 9	Usually 10
Pectoral fin rays	Usually 12 or 13	Usually 11
Vertebrae	Usually 29	Usually 28
Fleshy pad on lower lip	Absent	Developed
Subocular dark bar	Well developed; extends more downward than backward	Poorly defined; extends more backward than downward
Last two anal rays of adult male	Largely black	Tips only black
Margin of anal fin of adult female	Light	Dark
Vertical bands on body of adult female	Weak or absent	Several on urosome
Dark markings on lower side of adult female	A large triangular deep-seated dark blotch above anus	Several irregular superficial black spots above origin of anal fin
Gonopodium:		
Groove	Sinistral	Dextral
Length	42 to 56	58 to 63
Terminal swelling	None	Present, small
Ray 4p	Serrae on right half only	Serrae on both halves
Dorsal origin to snout tip:		
Males	50 to 57	56 to 61
Females	54 to 60	61 to 64
Dorsal origin to caudal base:		
Males	50 to 57	46 to 51
Females	45 to 53	42 to 46
Dorsal fin, depressed length:		
Males	39 to 47 (<i>pittieri</i>)	33 to 38
	30 to 39 (<i>amates</i>)	
Females	35 to 37 (<i>pittieri</i>)	29 to 33
	27 to 31 (<i>amates</i>)	
Pelvic fin length:		
Males	19 to 25	19 to 22
Females	20 to 24	16 to 18

males of the other; no such behavior was ever observed. In aquaria *amates* seems to be a more adaptable species than *fairweatheri* with regard to temperature and water chemistry. *P. fairweatheri* reproduced readily when first brought into the laboratory but the interval between broods gradually increased until after two years no further young were delivered. Some apparently healthy adults, though only a year old, became sluggish and died. Under the same conditions of aquaria, temperature, light and feeding, young male and female *amates* became sexually mature at three to four months, whereas those of *fairweatheri* required eight months or longer. We may infer that there are important physiological differences between these species.

***Phallichthys amates* (Miller)**

Diagnosis.—A robust, moderately deep-bodied,

small-headed species of *Phallichthys* without severely angular contours. Juveniles with a series of 2 to 6 narrow, vertical dusky bars along the side and flank, these well developed and more numerous, about 8 to 12, in adult males; poorly defined or absent in adult females. Adult females with a large, triangular black patch on either side above genital opening. Subocular dark bar well defined, extending more downward than backward across cheek. Tissue of lower lip not developed into a fleshy pad. Dorsal fin rounded, with a black margin; anal fin of female angulate, dusted with melanophores but with the margin pale. Gonopodium sinistrally folded, long and tapering but usually not extending beyond vertical from caudal base; without distinctive terminal swelling; with a single row of unpaired serrae on right half of ray 4p; dorsal margin of subdistal segments of ray 3 with minute

oblong or T-shaped denticles; left half of ray 3 with series of broad, flat spines, strongly incurved at tips only and tapering gradually to the 5 to 10 minute terminal elements; right half of ray 3 without definite spinous processes. Adult males with posterior two anal rays and associated membranes black. Gonopodial suspensorium with heavy, blunt uncini, their tips arched downward, emerging near tips of gonapophyses II and III; gonapophysis I without uncini or other bony processes. Teeth of inner series in narrow, gently curved bands that do not have lateral, posterior projections. Vertebrae usually 29, rarely 28 or 30. Scales in lateral series 26 or 27. Dorsal rays 8 to 11, first one or two simple. Anal rays 9, rarely 10. Pectoral rays 11 to 13. Head angle 45° to 53°.

The forms *amates* and *pittieri* appear not to be separable in their gonopodial or suspensorial structures, which are highly distinctive of other species of *Phallichthys* and *Carlhubbsia*. They differ from each other chiefly in dorsal and pectoral fin ray counts, in number of simple dorsal rays (Text-fig. 6), and in length of the dorsal fin. The structural separation is apparently not complete, however, and the habitat of the forms is presumably continuous through a yet uncollected coastwise region of northern Honduras and eastern Nicaragua (Map 1). Future field work will probably narrow or close the gap between the presently known ranges. If the diagnostic characters are found to be terminal elements of clines it may be necessary ultimately to unite *amates* and *pittieri* taxonomically; if they are sympatric and remain distinct, full specific status will be indicated. Provisionally the forms are treated as subspecies.

***Phallichthys amates pittieri* (Meek)**

Pl. III; Text-fig. 5

Poecilia pittieri.—Meek, 1912: 71-72 (original description; La Junta, Costa Rica).

Poeciliopsis pittieri.—Regan, 1913: 997 (La Junta, Costa Rica). Meek, 1914: 115-116 (swift rocky streams; La Junta, Parismina, Guapilis, and Virginia, Costa Rica). Henn, 1916: 120 (taxonomy; coloration). Alfaro, 1935: 237-238 (La Junta, Parismina, Río Molino, Guapilis, Costa Rica; description). Hildebrand, 1938: 309 (taxonomy; corrected distribution).

Phallichthys pittieri.—Hubbs, 1924: 10 (generic allocation; probable synonym of *P. amates*). Myers, 1925: 370 (distinct from *isthmensis* and *amates*). Hubbs, 1926: 70 (synonymy; Talamanca, Costa Rica; San San River, Almirante, Quebrada Nigra

DORSAL RAYS		PECTORAL RAYS					TOTAL
TOTAL	SIMPLE	22	23	24	25	26	
8	1	1	1	12			14
	2			1			1
9	1	1	2	94	2	3	102
	2			3			3
10	1			4	2	2	4
	2			7	4	26	37
11	1					1	1
	2			4	7	21	32
TOTAL		2	3	114 13	2 13	3 50	124 76

TEXT-FIG. 6. Frequency distribution of dorsal and pectoral fin ray counts in the subspecies of *Phallichthys amates*. In each box the number of specimens appears in the upper left for *P. a. amates*, in the lower right for *P. a. pittieri*.

[?=Nigra], Conquantu, Western Panama). Behre, 1928: 316 (synonymy; Skoon Creek, tributary to Río Tiliri, tributaries to Almirante Bay and Chiriqui Lagoon, western Panama). Hildebrand, 1930: 6 (Siquirres, Costa Rica; characters; taxonomy). Jordan, Evermann & Clark, 1930: 190 (synonymy, in part; type locality).

Poeciliopsis isthmensis.—Regan, 1913: 997, pl. 100 (original description; Colón, Panama). Meek & Hildebrand, 1916: 325 (Colón, Panama). ?Breder, 1925: 141 (Gatun Spillway, Panama; a young female, questionable reference).

Phallichthys isthmensis.—Myers, 1925: 370 (distinct from *pittieri* and *amates*).

Material.—CNHM 7841 and UMMZ 177277 (8 yg. to ad. males and females, 19 to 50 mm. standard length), Guapilis, Limón, Costa Rica, 1912, S. E. Meek; CNHM 7839 (paratypes of *Poecilia pittieri* Meek) (14 ad. males and females, 26 to 52 mm.), Río Reventazon, La Junta, Limón, Costa Rica, April 7, 1912, Meek; UMMZ 177276 and USNM 92157 and 92158 (29 ad. males and females, 20 to 41 mm.), Siquirres, Limón, Costa Rica, Oct. 12, 1928, A Alfaro; UMMZ 72585 (7 hf.-gr. to ad. males

TABLE 7. PROPORTIONAL MEASUREMENTS OF TEN ADULT MALES OF *Phallichthys amates pittieri*
Proportions are expressed in thousandths of the standard length.
See text for source of specimens.

Measurement	CNHM	UMMZ	USNM	UMMZ	CNHM	UMMZ	USNM 92158			
	7839	177277	94108	177277 (CNHM 7841)	7839	177276				
Standard length (mm.)	34.5	33.5	27.2	27.1	26.5	26.0	24.5	23.6	22.7	21.2
Body, greatest depth	383	388	331	328	377	346	327	318	352	330
Caudal peduncle, least depth	232	230	206	221	226	231	225	212	211	203
Dorsal origin to snout tip	522	543	529	517	509	538	498	508	533	566
Anal origin to mandibular symphysis	528	555	515	517	547	515	527	530	524	557
Dorsal origin to caudal base	554	567	537	517	566	538	555	517	520	557
Anal origin to caudal base	560	585	559	568	566	558	567	542	551	495
Head length	275	278	279	284	279	288	318	284	286	311
Head width	171	161	165	170	159	165	176	191	198	203
Snout length	78	84	85	77	75	77	...	85	75	80
Orbit length	90	84	103	96	94	96	98	97	97	94
Postorbital length of head	116	107	118	125	113	115	143	140	141	127
Orbit to angle of preopercle	61	75	70	66	68	69	69	68	66	71
Interorbital, bony width	133	119	118	125	125	123	131	140	141	132
Mouth, over-all width	99	104	92	89	98	108	...	102	...	104
Dorsal fin, depressed length	464	400	393	406	442	415	396	390	396	425
Anal fin, depressed length	545	513	507	531	559	558	486	525	551	552
Caudal fin length	371	331	360	343	385	369	383	373
Pectoral fin length	252	227	243	240	272	...	265	267	247	255
Pelvic fin length	223	239	202	203	234	238	245	212	238	212

TABLE 8. PROPORTIONAL MEASUREMENTS OF TEN ADULT FEMALES OF *Phallichthys amates pittieri*
Proportions are expressed in thousandths of the standard length.
See text for source of specimens.

Measurement	CNHM 7839									
Standard length (mm.)	52.0	49.0	46.8	45.5	45.4	44.0	38.6	35.0	34.6	33.0
Body, greatest depth	404	422	395	398	414	409	402	391	384	379
Caudal peduncle, least depth	223	227	214	215	220	216	207	214	202	212
Dorsal origin to snout tip	560	571	551	569	564	557	583	557	552	545
Anal origin to mandibular symphysis	650	665	645	659	641	639	661	663	647	639
Dorsal origin to caudal base	498	531	515	495	504	516	490	506	512	506
Anal origin to caudal base	435	416	415	424	412	416	391	403	410	415
Head length	267	271	271	266	271	280	277	297	280	285
Head width	194	206	192	191	200	200	187	186	182	158
Snout length	85	88	88	79	84	86	86	89	87	85
Orbit length	88	90	96	97	93	91	104	103	101	106
Postorbital length of head	117	114	111	112	110	111	109	114	116	121
Orbit to angle of preopercle	71	71	68	70	68	70	67	66	66	64
Interorbital, bony width	140	149	139	143	148	145	153	149	145	142
Mouth, over-all width	102	116	107	...	108	107	117	109	116	109
Dorsal fin, depressed length	352	371	368	356	357	364	352	351	364	364
Anal fin, depressed length	252	259	252	248	256	259	259	251	260	255
Caudal fin length	346	358	...	343	365	337	...	367
Pectoral fin length	240	249	239	235	249	245	259	249	237	255
Pelvic fin length	215	229	212	215	207	223	220	217	220	233

TABLE 9. PROPORTIONAL MEASUREMENTS OF TEN ADULT MALES OF *Phallichthys amates amates*
Proportions are expressed in thousandths of the standard length.
See text for source of specimens.

Measurement	UMMZ 173364			UMMZ 65220	UMMZ 173280			CNHM 56168	USNM 101780	UMMZ 113403
Standard length (mm.)..	29.0	28.0	28.0	25.5	24.8	22.5	20.0	19.7	16.0	14.0
Body, greatest depth....	407	411	411	373	383	382	365	360	313	322
Caudal peduncle, least depth	238	236	239	235	226	227	230	218	206	215
Dorsal origin to snout tip	562	578	571	565	544	578	560	584	506	572
Anal origin to mandibular symphysis	510	525	518	506	504	507	500	497	488	479
Dorsal origin to caudal base	472	486	489	549	504	560	525	492	481	479
Anal origin to caudal base	569	582	578	596	564	578	595	584	563	565
Head length	293	311	311	302	290	302	250	315	250	286
Head width	207	214	211	196	194	191	200	193	181	193
Snout length	107	103	107	78	81	76	80	96	113	93
Orbit length	93	96	96	94	97	102	105	102	100	107
Postorbital length of head	124	132	132	137	121	129	130	122	125	107
Orbit to angle of preopercle	76	75	75	63	60	67	70	66	44	43
Interorbital, bony width..	159	153	153	141	125	142	135	142	106	122
Mouth, over-all width...	117	121	114	114	101	111	110	96	100	107
Dorsal fin, depressed length	348	343	386	353	363	338	375	345	300	300
Anal fin, depressed length	466	475	479	478	...	480	490	533	475	544
Caudal fin length.....	345	378	411	...	375	378	380	386	300	329
Pectoral fin length.....	272	268	289	275	278	249	250	274	244	215
Pelvic fin length.....	234	250	239	235	234	200	215	233	200	193

and females, 23 to 37 mm.), Skoon Creek, tributary to Río Tiliri, tributary to Río Sixaola, Talamanca, Costa Rica, Jan. 25, 1923, E. Behre and Chambers; USNM 94201 (8 ad. males and females, 28 to 39 mm.), Descampos, 1200 meters, Costa Rica, 1928, A. Alfaro; USNM 94108 (4 ad. males and females, 25 to 41 mm.), Tiribi at 1,200 meters elevation, Costa Rica, May 7, 1928, A. Alfaro; UMMZ 72587 (3 ad. females, 34 to 52 mm.), San San Creek, tributary to San San River at old San San Farm, Bocas del Toro, Panama, Feb. 5, 1923, Behre and Chambers; UMMZ 72586 (4 hf.-gr. to ad. males and females, 29 to 51 mm.), Fruitdale Creek, along railroad spur back of Almirante, July and Aug., 1921, Behre; UMMZ 72588 (one yg., 14 mm.), Quebrada Nigra, flowing into Almirante Bay, Panama, July 8, 1921, Behre; UMMZ 72584 (one ad. female, 35 mm.), Guibari Creek, tributary to Río Cricamola, below Conquantu, Panama, Feb. 23, 1923, Behre and Chambers; UMMZ 72590 (4 ad. males, 24 to 33 mm.), Nomonuen Creek, tributary to Río Cricamola above Conquantu, Feb. 22, 1923, Behre and Chambers; UMMZ 72589 (one ad. male, 24 mm.), small creek tributary to right bank of Río

Cricamola below Conquantu, Feb. 26, 1923, Behre and Chambers.

Regan's (1913) record of this form from Colón was questioned by Hildebrand (1938), who stated that "Having collected rather extensively in 1911 and 1912, and again in 1935 and 1937, in the vicinity of Colón, from whence the types of *P. isthmensis* were reported, I am obliged to conclude that the species either is very rare there, or that a mistake was made in the earlier record."

Diagnosis. — A subspecies of *Phallichthys amates* with dorsal rays about equally 10 or 11, the first 2 rays (one only in 9% of specimens) simple in adult (Table 13 and Text-fig. 6). Pectoral rays 12 or 13, most often 13 (82% have 13 rays on at least one side). Dorsal fin larger than in *amates*: the depressed length 39 to 47% of standard length in adult males and 35 to 37% in adult females. Vertical bars usually present, though poorly defined, in adult females. Although our material of this subspecies averages larger than that of *P. a. amates*, the maximum sizes do not differ appreciably. The longest specimens examined are 40 mm. standard length

TABLE 10. PROPORTIONAL MEASUREMENTS OF TEN ADULT FEMALES OF *Phallichthys amates amates*
Proportions are expressed in thousandths of the standard length.
See text for source of specimens.

Measurement	UMMZ 173280				CNHM 56168		UMMZ 173280		CNHM 56168		UMMZ 173280	
	37.0	32.6	31.1	29.1	27.8	27.5	26.3	25.9	25.1	25.0		
Standard length (mm.) . . .	37.0	32.6	31.1	29.1	27.8	27.5	26.3	25.9	25.1	25.0		
Body, greatest depth	389	377	395	385	370	364	361	347	371	400		
Caudal peduncle,												
least depth	214	209	222	210	205	207	202	201	211	228		
Dorsal origin to snout tip	589	583	563	581	594	585	586	591	578	572		
Anal origin to mandibular symphysis	646	641	653	632	633	647	635	656	629	644		
Dorsal origin to caudal base	473	488	508	484	482	476	460	452	482	476		
Anal origin to caudal base	403	411	408	409	414	393	399	386	422	424		
Head length	303	307	302	299	309	309	304	313	307	296		
Head width	203	205	215	206	209	211	209	216	219	208		
Snout length	92	86	96	86	90	95	91	85	84	80		
Orbit length	97	95	100	103	112	102	103	104	108	104		
Postorbital length of head	124	132	135	127	137	135	137	131	135	140		
Orbit to angle of preopercle	62	67	64	76	72	69	65	69	76	76		
Interorbital, bony width . .	157	166	161	165	165	164	156	166	167	164		
Mouth, over-all width . . .	124	117	122	120	119	120	106	120	124	124		
Dorsal fin, depressed length	297	304	293	278	281	284	278	274	...	288		
Anal fin, depressed length	270	276	283	261	255	258	270	259	271	264		
Caudal fin length	346	350	354	333	353	367	346	351	374	356		
Pectoral fin length	257	245	264	251	259	258	247	251	239	264		
Pelvic fin length	224	227	231	227	205	200	198	201	203	224		

(male) and 52 mm. (female). Most adult males are between 22 and 34 mm. long.

Habitat.—Meek (1914) reported this form from swift rocky streams in Costa Rica, and specimens were collected by Alfaro at Tiribi and Descampos, Costa Rica, at altitudes of 1,200 meters; other stations are lower.

Range.—Known from the Caribbean slope of Costa Rica and western Panama (Map 1).

Phallichthys amates amates (Miller)

Pl. IV; Text-figs. 4, 5

Poecilia amates.—Miller, 1907: 108 (original description; Los Amates, Guatemala).

Poecilopsis amates.—Henn, 1916: 120 (taxonomy; gonopodium; coloration).

Phallichthys amates.—Hubbs, 1924: 10 (taxonomy; Tela, Honduras). Myers, 1925: 370 (distinct from *pittieri* and *isthmensis*). Hubbs, 1926: 70 (synonymy; records). Jordan, Evermann & Clark, 1930: 190 (synonymy, in part; type locality). Rosen & Gordon, 1953: 24, 29, 33, 38 (mechanics of gonopodium; sexual behavior).

Material. — *Guatemala*: UMMZ 65220,

CNHM 56168 (12 yg. to ad. males and females, 18 to 26 mm. standard length), Los Amates, Izabal, Jan. 17, 1905, N. Miller.

Honduras: UMMZ 173280 (25 yg. to ad. males and females, 15 to 37 mm.), Río Mapache at Masca, Cortes, April 5, 1951, Gordon and Wheeler; UMMZ 173297 (29 yg. to ad. males and females, 18 to 40 mm.), Río Tulian, Tulian, west of Puerto Cortes, Cortes, April 6, 1951, Gordon and Wheeler; USNM 101780 (one ad. male, 16 mm.), Río Chamelecón, 8 miles above San Pedro, Cortes, Jan. 19, 1936, Blanchard; UMMZ 173147 (8 yg. to ad. males and females, 12 to 24 mm.), Río Benejo, tributary to Río Chamelecón, just north of San Pedro Sula, Cortes, Mar. 18, 1951, Gordon and Chable; UMMZ 173156 (27 yg. to ad. males and females, 15 to 36 mm.), tributary to Río Ulua, Agua Priete, north of San Pedro Sula, Choloma Road, Cortes, Mar. 18, 1951, Gordon and Chable; UMMZ 56875 (one subad. male, 18 mm.), Tela, Atlantida, Mar. 14, 1923, T. H. Hubbell; UMMZ 113403 (one subad., 15 mm. and one ad. male, 16 mm.), river just outside of Tela, Atlantida, Spring, 1936, A. Greenberg; UMMZ 173177 (13 yg. to ad., 18 to 35 mm.), tributary to Río

TABLE 11. PROPORTIONAL MEASUREMENTS OF TEN ADULT MALES OF *Phallichthys fairweatheri*
Proportions are expressed in thousandths of the standard length.
See text for source of specimens.

Measurement	UMMZ	Holo-	UMMZ 144186							
	144186	type	28.7	27.4	25.5	25.5	25.5	25.5	24.0	23.0
		UMMZ								
		172456								
Standard length (mm.)..	30.1	29.7	28.7	27.4	25.5	25.5	25.5	25.5	24.0	23.0
Body, greatest depth....	415	438	411	394	392	412	361	404	354	348
Caudal peduncle, least depth	249	253	230	237	235	235	231	235	233	217
Dorsal origin to snout tip	598	606	610	584	588	588	588	596	567	565
Anal origin to mandibular symphysis	498	525	537	511	510	518	510	537	504	522
Dorsal origin to caudal base	498	495	495	493	482	506	471	471	496	461
Anal origin to caudal base	588	593	606	599	569	588	580	584	558	565
Head length	299	303	303	310	314	314	302	302	313	313
Head width	179	162	174	153	173	176	173	173	167	174
Snout length	86	88	91	88	86	90	90	90	83	87
Orbit length	106	101	105	99	110	106	110	114	104	109
Postorbital length of head	123	114	122	117	122	122	118	118	125	126
Orbit to angle of preopercle	63	61	63	66	67	71	71	63	63	65
Interorbital, bony width..	116	121	122	110	110	122	114	118	125	130
Mouth, over-all width...	100	98	91	91	94	94	94	98	88	87
Dorsal fin, depressed length	342	374	341	350	353	349	357	333	354	330
Anal fin, depressed length	585	606	610	602	580	596	608	624	617	622
Caudal fin length.....	365	380	366	365	392	373	373	377	371	369
Pectoral fin length.....	239	253	230	230	239	247	254	261
Pelvic fin length.....	219	202	195	201	212	196	196	212	204	196

Lancetilla, 1 mile south of Tela, Atlantida, Mar. 20, 1951, Gordon and Chable; UMMZ 173193 (1 ad. female, 29 mm.), Río Lancetilla at Lancetilla near Labor Camp swimming pool, near Tela, Atlantida, Mar. 22, 1951, Gordon and K. J. Davidson; UMMZ 173206 (20 yg. to ad., 15 to 39 mm.) and UMMZ 173214 (24 hf.-gr. to ad. males and females, 14 to 36 mm.), Lily Pond, Lancetilla Experimental Station, Lancetilla, near Tela, Atlantida, Mar. 22, 1951, Gordon and Davidson; UMMZ 173231 (246 yg. to ad., 15 to 37 mm.), drainage ditch on Sec. 8, African Oil Palm Plantation, San Alejo, Atlantida, Mar. 24, 1951, Gordon and Davidson; UMMZ 173221 (26 yg. to ad., 14 to 47 mm.), tributary to Río San Alejo, San Alejo, Atlantida, Mar. 24, 1951, Gordon and Davidson; UMMZ 173344 (35 yg. to ad., 14 to 30 mm.), near San Juan Benque, 48.5 km. west of La Ceiba, Atlantida, April 11, 1951, Gordon, Chable and George; UMMZ 173356 (6 hf.-gr. to ad., 20 to 27 mm.), near San Juan Benque, 47.3 km. west of La Ceiba, Atlantida, April 11, 1951, Gordon, Chable and George; UMMZ 173364 (63 yg. to ad., 19 to 39 mm.), Río Cuero, near La Masica, Atlantida, April 11, 1951, Gordon,

Chable and George; UMMZ 173372 (29 yg. to ad., 18 to 37 mm.), Río Salado canal, Atlantida, April 11, 1951, Gordon, Chable and George; UMMZ 173318 (20 yg. to ad., 17 to 56 mm.), stream 6.6 km. east of La Ceiba, at Standard Fruit Company, Atlantida, April 10, 1951, Gordon and Chable; UMMZ 173329 (149 yg. to ad., 11 to 43 mm.), 18.3 km. E. of La Ceiba, Atlantida, April 10, 1951, Gordon and Chable.

Diagnosis.—A subspecies of *Phallichthys amates* with dorsal rays 8 to 10, usually 9 (10 in 4% of specimens), the first ray (2 rays in 3% of specimens) simple in adult (Table 13 and Text-fig. 6). Pectoral rays 11 to 13, usually 12 (only 4% have 13 rays on one or both sides). Dorsal fin smaller than in *pittieri*; the depressed length 30 to 39% of standard length in adult males and 27 to 30% in adult females. Vertical bars not evident in adult females. The longest specimens examined are 30.6 mm. standard length (male) and 56 mm. (female). Most males are between 20 and 30 mm. long.

Habitat.—As judged from the field records of Myron Gordon during 1951 in Honduras, this

TABLE 12. PROPORTIONAL MEASUREMENTS OF TEN ADULT FEMALES OF *Phallichthys fairweatheri*
Proportions are expressed in thousandths of the standard length.
See text for source of specimens.

Measurement	UMMZ 144186	Allo- type UMMZ 172457	UMMZ 144186							
			33.0	31.8	31.2	31.0	29.5	28.6	28.5	27.1
Standard length (mm.)..	38.3	33.3	33.0	31.8	31.2	31.0	29.5	28.6	28.5	27.1
Body, greatest depth....	381	408	382	377	394	406	390	388	379	387
Caudal peduncle, least depth	225	216	221	204	218	210	220	220	218	214
Dorsal origin to snout tip	632	616	639	613	615	629	631	626	628	635
Anal origin to mandibular symphysis	674	666	651	670	683	690	671	682	667	668
Dorsal origin to caudal base	423	453	445	425	445	442	447	437	432	432
Anal origin to caudal base	418	423	406	396	417	400	417	395	421	410
Head length	313	324	324	321	330	332	325	332	337	336
Head width	183	189	191	186	192	203	193	192	193	199
Snout length	94	99	91	94	96	100	95	94	102	100
Orbit length	110	111	109	113	109	116	112	112	116	122
Postorbital length of head	133	132	133	126	128	139	136	140	133	140
Orbit to angle of preopercle	57	66	61	63	64	65	68	66	63	63
Interorbital, bony width..	151	159	152	154	154	161	159	161	158	162
Mouth, over-all width...	99	105	106	101	103	106	102	112	116	103
Dorsal fin, depressed length	300	309	303	305	304	294	322	294	309	295
Anal fin, depressed length	264	279	267	252	...	281	...	269	274	273
Caudal fin length.....	352	360	361	368	...	361	366	367	375	365
Pectoral fin length.....	...	243	239	...	250	239	254	252	246	244
Pelvic fin length.....	172	171	173	179	173	174	170	168	175	166

TABLE 13. FREQUENCY DISTRIBUTION OF DORSAL FIN RAYS IN *Carlhubbsia* AND *Phallichthys*

Species or Subspecies	Total Dorsal Rays				Simple Dorsal Rays	
	8	9	10	11	1	2
<i>Carlhubbsia stuarti</i>	5	116	2		1	19
<i>Carlhubbsia kidderi</i>	1	19				20
<i>Phallichthys amates pittieri</i>			45	37	7	72
<i>Phallichthys amates amates</i>	16	108	5		124	4
<i>Phallichthys fairweatheri</i>		31	11		39	2

form has rather broad tolerance to amount of current and type of bottom. At stations where moderate to large samples were taken, the current was recorded variously as none, slight, swift and rapid; the bottom as mud, mud and sand, hardpan and rubble; the water as clear, brown, stagnant and brown, and cloudy; vegetation (representing several species) as wanting or present; temperatures varied from 22° to 28° C. All specimens were seined from shallow water, usually less than three feet deep.

Range.—Known from the Atlantic coastal lowland of the Motagua River system, eastern Guatemala, east to near La Ceiba, north-central Honduras (Map 1).

Phallichthys fairweatheri, n. sp.

Pls. V, VI; Text-figs. 2, 4, 5

Dextripenis evides (*nomen nudum*).—Turner, 1940: 89 (superfetation). Scrimshaw, 1944: 182 (superfetation). Scrimshaw, 1945: 234-241 (embryonic development). Scrimshaw, 1946: 21-22 (unnamed form from Guatemala; egg size).

Material.—Holotype (UMMZ 172456), an adult male, 29.7 mm. in standard length, collected in Río San Pedro de Mártir, or a branch, about ¼ mile below Laguna de Yalác, some 6 leagues (by river) upstream (east) from El Paso de los Caballos, in the Usumacinta River

basin, El Petén, Guatemala, on March 18, 1935, by Carl L. Hubbs and Henry van der Schalie. The allotype (UMMZ 172457), an adult female, 33.3 mm. long, and 6 additional half-grown to adult specimens (UMMZ 144191, 21 to 42 mm. long, were taken with the holotype (see Map 2). Additional specimens are as follows:

Río San Pedro de Mártir drainage (El Petén, Guatemala): UMMZ 144190 (19 hf.-gr. to ad. males and females, 13 to 44 mm.), Laguna de Yalác, in course of Río San Pedro de Mártir about 6 leagues by river (east) above El Paso de los Caballos, in front of old chicle station, Mar. 16, 1935, Hubbs and van der Schalie; UMMZ 144189 (76 hf.-gr. to ad. males and females, 19 to 42 mm.), Laguna de Yalác, both sides of old chicle station, Mar. 16-17, 1935, Hubbs and van der Schalie; UMMZ 144188 (one hf.-gr. and one female, 15 and 35 mm.), lagoon-like arm of Río San Pedro de Mártir at El Paso de los Caballos, March 10-14, 1935, Hubbs and van der Schalie; UMMZ 144186 (792 yg. to ad. males and females, 12 to 40 mm.), Río San Pedro, at or opposite Desempeño, just below El Paso de los Caballos, Mar. 12, 1935, Hubbs.

Río de la Pasión drainage (El Petén, Guatemala): UMMZ 144185 (9 hf.-gr. to subad., 16 to 19 mm.), Laguna de Eckibix, in savanna region southeast of Santa Ana on south shore about ¼ mile from west end, Feb. 26, 1935, Hubbs and van der Schalie; UMMZ 144187, (3 hf.-gr. to ad. females, 11 to 19 mm.), Laguna de Eckibix, extreme west end, Feb. 26, 1935, Hubbs; UMMZ 144193 (44 hf.-gr. to ad. males and females, 15 to 39 mm.), Arroyo Subín, at Trinidad, about 2 miles east of Santa Teresa, April 2, 1935, Hubbs and van der Schalie; UMMZ 144197, 144194, and 144192 (77 yg. to ad. males and females, 11 to 37 mm.), Arroyo Subín at Santa Teresa, 13 miles south of La Libertad, April 2-3, 1935, Hubbs, van der Schalie and Taintor; UMMZ 144195 (70 yg. to ad. males and females, 12 to 32 mm.), Arroyo Subín, at second rapids (about 2 miles) above mouth into Río de la Pasión, April 25, 1935, Hubbs; UMMZ 144196 (7 hf.-gr. to ad. males and females, 19 to 36 mm.), Arroyo Subín, in small bay connected with stream beside third rapids (about 2½ miles) from mouth into Río de la Pasión, April 25, 1935, Hubbs.

New River drainage (British Honduras): NYZS-GAF 5 (49 yg. to ad. males and females, 11 to 30 mm.), Hill Bank opposite campsite, inlet to lagoon of New River, Mar. 16, 1954, Gordon, Williams and Hamilton.

Río Hondo drainage (British Honduras): NYZS-GAF 6 (71 yg. to ad. males and females,

TABLE 14. FREQUENCY DISTRIBUTION OF ANAL FIN RAYS IN THE FORMS OF *Carlhubbsia* AND *Phallichthys*

Species or Subspecies	Anal Rays		
	9	10	11
<i>Carlhubbsia stuarti</i>		19	1
<i>Carlhubbsia kidderi</i>	1	18	1
<i>Phallichthys amates pittieri</i>	79		
<i>Phallichthys amates amates</i>	25	2	
<i>Phallichthys fairweatheri</i>		22	

12 to 32 mm.), lagoon and creek on east bank of east branch of Río Hondo, opposite San Antonio, Orange Walk, Mar. 20, 1954, Gordon, Fairweather and Chaveria; NYZS-GAF 7 (123 yg. to ad. males and females, 11 to 31 mm.), lagoon opposite San Antonio, connected with creek to east branch of Río Hondo, Orange Walk, Mar. 21, 1954, Gordon and Chaveria.

Diagnosis.—A deep-bodied, large-headed species of *Phallichthys* with severely angular contours. There is a series of 2 to 4 broad dusky bars on the caudal peduncle that may fuse ventrally to form a conspicuous postanal blotch, especially pronounced in adult males. In both sexes, from 6 to 7 rows of bright orange dots extend along scale rows from opercle to caudal base.³

Adult females with several small and irregular black spots above genital opening. Usually with an indistinct subocular dark bar that extends more backward than downward across cheek. Tissue of lower lip developed into a fleshy pad. Dorsal fin rounded, with a black margin, the middle rays longest. Anal fin of female angulate, with conspicuous dark border. Gonopodium dextrally folded, long and tapering, exceeding vertical from caudal base, with a minute terminal swelling of tough membranous tissue; ray 4p with a single row of large, retrorse proximal serrae and smaller erect terminal serrae on left half and 5 or 6 minute serrae on right half; dorsal margin of ray 3 without denticles; right half of ray 3 with series of broad, flat spines, not much incurved and tapering abruptly to the 8 or 9 slender terminal segments; left half of ray 3 without definite spinous processes. Adult males with tips of posterior anal rays black. Gonopodial suspensorium with recurved uncini, when present, developed near base of gonapophysis I and heavy subtriangular uncini near

³ Red and yellow pigments are water soluble and for this reason are not observed in preserved specimens. The color description is taken from living and recently fixed animals from British Honduras.

TABLE 15. FREQUENCY DISTRIBUTION OF PECTORAL FIN RAYS IN THE FORMS OF
Carlhubbsia AND *Phallichthys*
The counts from left and right fins for each specimen are summed

Species or Subspecies	Pectoral Rays									
	18	19	20	21	22	23	24	25	26	27
<i>Carlhubbsia stuarti</i>									19	1
<i>Carlhubbsia kidderi</i>	3	..	13	2						
<i>Phallichthys amates pittieri</i>							14	13	51	
<i>Phallichthys amates amates</i>					3	3	115	2	3	
<i>Phallichthys fairweatheri</i>			5	4	10	..	1			

TABLE 16. FREQUENCY DISTRIBUTION OF SCALES IN LATERAL SERIES IN THE FORMS OF
Carlhubbsia AND *Phallichthys*

Species or Subspecies	Lateral Scales					
	22	23	24	25	26	27
<i>Carlhubbsia stuarti</i>				11	9	
<i>Carlhubbsia kidderi</i>					6	14
<i>Phallichthys amates pittieri</i>					13	62
<i>Phallichthys amates amates</i>					28	6
<i>Phallichthys fairweatheri</i>	5	13	4			

TABLE 17. FREQUENCY DISTRIBUTION OF CIRCUMFERENTIAL SCALES IN THE FORMS OF
Carlhubbsia AND *Phallichthys*

Species or Subspecies	Scale Rows Around Body					
	21	22	23	24	25	26
<i>Carlhubbsia stuarti</i>			2	4	10	4
<i>Carlhubbsia kidderi</i>		9	8	3		
<i>Phallichthys amates pittieri</i>		13	7			
<i>Phallichthys amates amates</i>	1	9	9	1		
<i>Phallichthys fairweatheri</i>	1	10	9	2		

tip of gonapophysis II; uncini near tip of gonapophysis III, when present, short, heavy and sharply pointed. Teeth of inner series in broad, strongly curved bands that have well-developed, lateral, posterior projections. Vertebrae usually 28, infrequently 27 or 29. Scales in lateral series 22 to 24. Dorsal fin rays 9 or 10, usually 9, typically with only the first ray simple, rarely with 2 simple rays. Anal fin rays 10. Pectoral fin rays 10 or 11, rarely 12. Head angle 41° to 49°.

For the distinctive features of body and fin form, pigmentation and skeletal morphology, see also Tables 6, 11-18.

General Description.—A deep-bodied, robust species with high, severely angular contours. In adult males the predorsal profile is flat and rises sharply to the dorsal origin; the dorsal and ventral margins of the caudal peduncle are

straight and taper rather abruptly to the caudal base. The head angle is 41° to 49°. In adult females the predorsal profile rises less sharply to the dorsal origin; the dorsal and ventral margins of the caudal peduncle slope gently toward the plane of the body axis and taper only gradually toward the caudal base. The head angle is 41° to 46°. In both sexes the snout is distinctly pointed and long, and the head deep and triangular in profile. The sharply-pointed appearance of the snout in profile view is due, in part, to the development along the outer margin of the lower jaw of a variously developed fleshy pad. In general the male is relatively deeper than the female and has conspicuously rhombic contours; those of the female are more curvilinear.

The median elevated fins in adult females originate slightly closer to the base of the caudal peduncle than to the tip of the snout and are

nearly opposite. In adult males the anal fin or gonopodium originates slightly in advance of the more posteriorly inserted dorsal fin and this is essentially the median position with reference to the body axis. The dorsal fin in both sexes is broadly rounded; the middle and posterior rays exceed the anterior ones in the depressed fin. In males the fin is more elevated and may extend almost to the caudal base. In females the anal fin has an acute anterior angle, the free margin somewhat falcate, and the third and fourth rays are much the longest. The tip of the fully developed gonopodium of the adult male extends backward to slightly beyond the caudal base. The caudal fin in both sexes is broad, subtruncate, only slightly rounded at its upper and lower posterior margin. There are 15 or 16 principal caudal rays. The rounded pelvic fins in adult females are small, about one-half the length of the anal fin; they originate approximately one-third the distance from the anal origin to the lower edge of the subopercle. In adult males pelvic rays 2 and 3 are produced; they originate just anterior to the origin of the gonopodium. The pectoral fins are broadly spatulate in both sexes and originate well below the midlateral line just behind the opercular margin, extending backward to a vertical from the dorsal origin.

The gillrakers on the outer face of the first arch, though well developed, are short and slender; they number 20 to 25.

There are three principal pigment patterns on the trunk and caudal peduncle. Two are produced by melanophores: a reticular pattern that is usually most evident above the midlateral line, and a series of vertical bars that is more pronounced in the adult male. The bars are more or less uniform and are restricted largely to the caudal region, only one or two bars of a series of 6 or more being situated anterior to the vertical from the anal origin. Two or three of the posterior bars are darker at their upper and lower extremities than midlaterally, and may ring completely the caudal peduncle. Ventrally the bars, particularly in adult males, may be so intensely black and broad that they fuse to form a large, postanal blotch. Lateral striping consists of 6 to 7 rows of bright orange dots that extend along the scale rows from the opercle to the caudal base. Adult females have three or more irregular but intensely black spots just above the anal base. In adult females both elevated median fins are evenly edged with black, except for the tips of the first three or four anal rays. In adult males the dorsal fin is black-edged; the gonopodium is unmarked, except for a stippling of melanophores and erythrophores at its base, but the tiny posterior anal rays have black

TABLE 18. FREQUENCY DISTRIBUTION OF NUMBER OF VERTEBRAE IN THE FORMS OF *Carlhubbsia* AND *Phallichthys*

Species or Subspecies	Vertebrae			
	27	28	29	30
<i>Carlhubbsia stuarti</i>		23		
<i>Carlhubbsia kidderi</i>		2	36	3
<i>Phallichthys amates pittieri</i>		1	53	1
<i>Phallichthys amates amates</i>		1	19	1
<i>Phallichthys fairweatheri</i>	1	36	2	

tips. The other fins are without distinctive color pattern, but may show a fine dusting of melanophores, xanthophores and erythrophores, especially near their bases. The lips and the interorbital region are suffused evenly by melanophores. A short and faint suborbital bar is occasionally present.

Skeletal Morphology.—The vertebral axis, consisting usually of 28 elements (Table 18), is divided approximately in half into a precaudal or trunk series and a caudal series, the division being determined by the first hemal spine. In adult females, the first hemal spine usually emerges from the 15th vertebra. In adult males, the first attached hemal spine, which becomes sexually modified to form the first gonopophysis of the gonopodial suspensorium, is on the 14th vertebra. The precaudal portion of the axis rises gently from the vertebral centrum carrying the first hemal and then flattens out again as it approaches the base of the skull. The vertebral axis takes the form of a gentle sigmoid curve, the spinal curvature being especially pronounced in large adults. A pleural rib is present on each precaudal vertebra except the first. The first rib is long and slender and is loosely articulated with the postero-distal margin of the transverse process of the second vertebra; the rib lies against the medial surface of the pectoral girdle. Near the distal end of the rib there lies an expanded, stylet-shaped bone (see p. 7), the "postcleithrum." Each successive rib is joined to a vertebra in the same manner as the first rib; they gradually diminish in size posteriorly. In adult males the last 6 or 7 ribs become sexually modified. The last three are quite small, slender and widely separated; the preceding three or four ribs arch gently forward at their tips and converge, just above and behind the pelvic girdle. Minute epipleurals are joined loosely with the postero-proximal surfaces of the pleural ribs just below or adjacent to the level of the transverse processes; they are present on all but the last two pleural ribs. Parapophyses (see p. 7)

do not occur on any of the anterior caudal vertebrae in *Phallichthys fairweatheri*.

The contribution of the vertebral axis to the gonopodial suspensorium of the adult male consists of four specialized hemal spines. The first, or ligastyle, is a long, slender rod that lies in the primary suspensory ligament. Its dorsal detached margin migrates forward during sexual differentiation and comes to lie beneath the centrum of the 10th precaudal vertebra. The next three hemal spines or gonapophyses are specialized chiefly by the addition of bony substance to their distal and posterior surfaces. The first inclines slightly forward. It is straight except for the distal fourth which is bent sharply forward to meet the dorsal edge of the primary gonactinostal complex. A single pair of well-developed curvilinear uncini is usually present; they extend backward from the base of gonapophysis I and overlap the base of gonapophysis II. The second gonapophysis is more or less vertical. The base of the spine's shaft is slender, but it widens gradually toward the tip where it merges with a pair of extremely heavy, subtriangular uncinate processes. The third gonapophysis is either vertical or inclines slightly backward. It is the longest of the three gonapophyses, and its uncini, when present, are quite small, subtriangular, and are always situated near the distal tip of the spine's shaft. The actinosts of the anal fin in the adult male also are specialized and are incorporated into the suspensorial system as the gonactinosts. The first is a short, heavy, blunt rod that inclines sharply forward. It articulates with fin rays 1 and 2. Gonactinosts 2, 3 and 4 are fused to form a single highly complex plate of bone, the primary gonactinostal complex, which supports fin rays 3, 4 and 5. The complex in this species is compressed antero-posteriorly. The posterior lateral wings that are produced symmetrically outward from eccentric positions along either side of the core of gonactinost 4 are scarcely developed except at the dorsal third where they flare broadly. Gonactinost 5 lies embedded in the depression formed by the lateral wings of the primary complex. Gonactinosts 6, 7, 8 and 9 are slender and rod-like; their tips flare apart. Actinost 10 of the anal fin becomes much reduced and is incorporated into gonactinost 9 as a tiny sliver of bone. The gonactinosts are firmly anchored to the vertebral axis by means of the ligastyle and the gonapophyses. The primary gonactinostal complex is attached by ligaments to the ventral margins of the ligastyle and gonapophysis I. The tip of gonapophysis II interdigitates with gonactinosts 7 and 8, where it is held in place by means of tendons and ligaments. The tip of gonapophysis III curves

forward toward the posterior surface of the final gonactinost, where it, too, is attached by means of ligamentous connective tissues.

The gonopodium in the adult male consists of the produced and modified rays 3, 4 and 5 of the anal fin. Together these rays are folded to form a hemicylinder with a broad groove along the right side of the gonopodium. When held at rest, i.e., pointed caudally, ray 3 forms the ventral border, ray 5 the dorsal border and ray 4 the lateral wall of the dextral trough. The paired halves of ray 3 are segmented to the tip of the fin and are never consolidated. The broad and flat spinous processes of the subterminal 20 to 30 segments of the right half of ray 3 are only slightly dextrally incurved to form the ventral border of the open groove; they taper abruptly to 8 or 9 paired terminal segments that form a hooked ramus. Definitive spines are wanting on the left half of ray 3 and the individual, relatively unspecialized, segments are shallow and rather poorly developed. The subterminal segments of ray 4a are flattened dorso-ventrally and their long axes are greatly extended. The terminal 10 or 11 shorter segments are closely applied to the dorsal margin of the hooked distal ramus of ray 3. A loaf-shaped membranous swelling arises from the right side of the composite terminal bony ramus. The proximal segments of the right half of ray 4p form a high, knife-like ridge. Penultimately at the distal fourth of the left half of ray 4p there is a series of approximately 15 retrorse serrae that face upward and outward away from the fin's long axis; they are preceded by 4 or 5 smaller, slender and erect, terminal serrae that extend laterally at right angles to ray 5. The elements of the distal fourth of the right half of ray 4p are delicate and thread-like except where they are modified as a series of 5 or 6 minute retrorse serrae adjacent to the bases of the larger serrae on the left half of this ray. Ray 5a is bilaterally asymmetrical; the segments of the right half of the ray are wider and more flattened than those of the left half. The segments of both, however, are greatly dilated longitudinally and extend to the tip of the fin beneath the membranous swelling as slender hair-like rods. The segments of ray 5p are extremely delicate. They are joined to the outer edges of the paired members of 5a below; those of the left half are poorly developed, becoming obsolescent at the level of the minute serrae on the right half of ray 4p; the right half of ray 5p is developed as a high, laterally compressed ridge that extends distally to the level of the smaller, erect serrae at the tip of the sinistral component of 4p. The tips of all the rays become rather slender distally

and at the extreme tip of the fin they form the beginnings of a tight spiral in which the uppermost or 5th ray shows the greatest displacement from its original axis. The gradual decrease in height of all bony elements toward the tip of each ray gives to the gonopodium as a whole a distinctly acuminate profile. Other than the hooked distal rami of rays 3 and 4a there is no distinctive terminal segment.

Relationships.—This new species is referable to the genus *Phallichthys* on the basis of the structure of the gonopodium and gonopodial suspensorium (see Text-figs. 4 and 5, and discussion on pp. 29-32). It may be separated readily from the only other known species, *P. amates*, by the characters listed in the diagnoses and in Table 6. The two species are allopatric (Map 1).

Nomenclature.—*Phallichthys fairweatheri* was first collected by C. L. Hubbs in El Petén, Guatemala. Hubbs thought that this fish should be the type of a new genus and assigned it the unpublished manuscript name "*Dextripenis evides*," the generic name referring, of course, to the dextrally folded gonopodium. Specimens bearing this name were made available to C. L. Turner and N. S. Scrimshaw for their investigations on the reproductive behavior of poeciliid fishes. Both men used the name or otherwise referred to this species in their studies (see synonymy, p. 24), but did not accompany it with an adequate description. Thus, *Dextripenis evides* is a *nomen nudum* and has no validity under the International Rules of Zoological Nomenclature.

This species is named in honor of the Rev. Gerald Fairweather in acknowledgment of his participation in obtaining extensive scientific collections of fishes in British Honduras.

Range.—*Phallichthys fairweatheri* is known to occur in three apparently separated areas in British Honduras and northern Guatemala (Map 1). The fish from the Río Hondo and New River systems, tributary to Chetumal Bay, British Honduras, probably represent a single stock since these drainages are connected by flood plains at high water, according to L. C. Stuart (personal communication). The stocks in the Río de la Pasión and Río San Pedro de Mártir systems of Guatemala are now well separated, but future collecting in the connecting waters of the Río Usumacinta system (Map 2) may close this gap.

Habitat.—In 1935, Drs. Carl L. Hubbs and Henry van der Schalie, on the Fifth Carnegie Institution-University of Michigan Expedition, took this species 13 times in El Petén. At all

stations the water was quiet or stagnant, or at least some quiet water was present. The water was clear, often blackish, at most stations though dirty at a few; vegetation was commonly present and often dense. The bottom consisted of or included soft mud at all stations. The habitat is perhaps best indicated by the conditions in Río San Pedro de Mártir (UMMZ 144186), where 792 specimens were taken: water rather dirty; vegetation slight to thick; bottom very soft mud with much hydrogen sulphide; virtually no current; shore a recently exposed mudflat.

ASSESSMENT OF TAXONOMIC CRITERIA

The species of *Carlhubbsia* and *Phallichthys* are so similar in appearance that early in this study we thought they constituted a single genus. Largely on the basis of the detailed anatomical differences in the gonopodium and gonopodial suspensorium discussed below, we conclude not only that generic separation is called for, but that two distinctive phyletic lines are involved. The common feature of an asymmetrically folded gonopodium is believed to be independently evolved in these lines.

Gonopodium

The gonopodia of *Carlhubbsia* and *Phallichthys* are permanently folded to one side (sinistrally in *P. amates*, dextrally in other species), and show little internal symmetry. Although the gonopodia are superficially similar because of asymmetry, for a phylogenetic study it is essential to obtain more detailed information on individual gonopodial structures. To this end, special attention is directed to form and frequency of specialized terminal features. Some of the salient distinctions between the gonopodia of these genera are set forth in Table 19 (see also Text-figs. 3 and 4). More extended descriptions and discussions of gonopodial characteristics appear in the systematic accounts of genera and species.

In both genera the elements in ray 3 reflect the over-all symmetry of the fin, as do all the bony elements of the gonopodium. Segments which abut directly onto the permanently developed groove along one side of the fin, and which are functional components of this groove, are generally better developed than segments which arise on the side away from the direction of folding. Thus, in the sinistral *Phallichthys amates*, the dextral spinous segments near the tip of ray 3 are short with miniscule ventral processes, whereas the sinistral elements are long and curved, the ventral processes folding inward to form the ventral margin of the gonopodial groove. In *P. fairweatheri* and the species of

Carlhubbsia the spines are present only on the right half of the ray and face into the gonopodial groove, again to form the ventral margin of the partially closed channel. An exception to this generalization involves those specialized hold-fast structures that are believed to assist in copulation; for example, the distal serrae on ray 4p in all four species face outward, that is, away from the gonopodial groove on the convex surface of the permanently folded fin.

In *Phallichthys* the gonopodium is comparatively simple, having few specialized terminal features; there are unilateral distal spines on ray 3 and serrae on ray 4p, the subterminal elements of all rays are uniformly simple and the fifth ray is unspecialized (Table 19). In *Carlhubbsia*, by comparison, the gonopodium is complex. Each ray with the exception of the anterior branch of 5 is terminated by a series of specialized elements: in addition to spines on ray 3 and distal serrae on ray 4p there is a small terminal hook on ray 3, a series of laterally dilated terminal segments on ray 4a, a disrupted ray 4p and posterior serrae on ray 5p.

Gonopodial Suspensorium

In poeciliid fishes the development of such suspensorial structures as the ligastyle and the gonapophyses is influenced by over-all growth patterns and time and rate of sexual differentiation (Rosen, ms.). Growth and maturation, in turn, are affected by a variety of environmental factors, such as nutrition, light and temperature. But underlying genetic patterns appear largely to control the expression of some structures irrespective of body size or form; if these can be properly identified they provide indications of natural relationship. The position of uncini on the gonapophyses and their form, as well as the shape of the primary gonactinostal complex, have always proved to be relatively constant within a related group of species.

The form of the ligastyle and the orientation of the gonapophyses are apparently controlled in large part by the form of the body. In *Carlhubbsia kidderi*, the slenderest of the species under consideration, the ligastyle is reduced to a rudiment of bone embedded in the primary suspensory ligament and all three gonapophyses incline forward at a sharp angle. In *Phallichthys amates*, of intermediate body depth, the ligastyle is quite small but in some individuals is prolonged into a slender rod of bone equal in length to the diameter of a vertebral centrum; only the first gonapophysis is bent sharply forward. In *C. stuarti* and *P. fairweatheri*, the two deepest-bodied species, the ligastyle is a well-developed,

long bony rod and the anal fin supports have a more nearly vertical orientation. In each, the angle between the gonapophyses and the vertebral column is roughly proportional to the distance between the gonactinosts and the vertebral axis (Text-fig. 5).

Positional relationships and form of the uncini on the three gonapophyses have proved extremely effective in interpreting the relationships in these fishes. As may be seen from Plate VI, Text-fig. 5, and Table 19, there is measurable individual variation within species and between species of *Carlhubbsia* and *Phallichthys* in the orientation and extent of development of uncini. But what matters from the viewpoint of mechanical control is not the precise point at which an uncinus arises *per se*, but the total adaptation for the job of suspension, which if the point is constant can be achieved by fine adjustments in size, orientation and rigidity of the uncini. In the species of *Carlhubbsia*, for example, *C. stuarti* lacks uncini on gonapophysis III, but the uncini on gonapophysis II are so long that they overlap the shaft of number III at the same point at which two tiny uncini arise on element III in *C. kidderi*. Two specimens of *C. kidderi* were found with well developed uncini on gonapophysis II, but none on III. The same broad functional problem of suspension has been solved repeatedly in different ways within the Poeciliidae as a whole. For this reason it is significant that, despite individual and specific differences, each genus presents a relatively distinctive pattern with respect to the topographic relations and basic morphology of these gonapophyseal processes.

In both *Carlhubbsia* and *Phallichthys* the relative size of the primary gonactinostal complex remains fairly constant, without reference to variations in body proportions or ultimate size attained. As a result, in the more slender species, *C. kidderi* and *P. amates*, this bony complex closely approaches the vertebral axis, whereas in the deep-bodied forms, *C. stuarti* and *P. fairweatheri*, it is well separated. As previously noted, the length of the ligastyle and the angle of inclination of the first gonapophysis compensate for these differences. Thus, the relative constancy within each genus suggests conservatism in the gonactinostal complex, and the finding of differences between the groups of species (genera) emphasizes its reliability. In the species of *Carlhubbsia* the primary complex is greatly dilated along the antero-posterior dimension; in the species of *Phallichthys* it is narrow (Text-fig. 5). This difference is brought about in three ways: when incorporated into the complex acti-

TABLE 19. SIGNIFICANT CONTRASTING CHARACTERS OF *Carlhubbsia* AND *Phallichthys*

Character	<i>Carlhubbsia</i>	<i>Phallichthys</i>
Gonopodium (adult male):		
Ray 3	15 to 20 subterminal segments with flattened incurved spinous processes; 5 to 8 distal elements simple; with small curved terminal hook	20 to 30 subterminal segments with flattened incurved spinous processes; 8 or 9 distal elements simple, forming a ventrally hooked ramus; no terminal hook
Ray 4a	Approximately 15 distal segments much elevated; not forming a hooked ramus	5 terminal segments compose a minute hooked ramus that arches downward over the hooked tip of ray 3
Ray 4p	Very thin distally, closely joined to ray 4a; obsolete from segments 20 to 25 of ray 4a (counting apico-basally) to about segment 15 (ray 4a) where it reappears as a clustered series of 4 to 8 unpaired retrorse serrae	Terminal series of up to 17 or 18 well-developed, retrorse serrae
Ray 5	Ray 5p with sinistral, retrorse serrae on 6 or 7 (<i>kidderi</i>) or about 15 (<i>stuarti</i>) terminal segments; serrae fused with distal elements of 5a and separated from unspecialized segments of 5p (<i>kidderi</i>) or distinct and continuous with unspecialized segments (<i>stuarti</i>)	Little specialized except in symmetry; without serrae
Gonapophyses (adult male):		
Uncini on I	Slender and straight, tilted downward, of moderate length (<i>kidderi</i>) or long (<i>stuarti</i>); arising near base of gonapophysis	Slender and short, curved upward, arising near base of gonapophysis (<i>fairweatheri</i>) or absent (<i>amates</i>)
Uncini on II	As on gonapophysis I but longer and stronger, situated slightly farther down gonapophysis but in same plane as uncini on I	Stout, broad based, short, curved downward, arising on distal half of gonapophysis; not in same plane as uncini on I
Uncini on III	Absent (<i>stuarti</i> , rarely in <i>kidderi</i>) or rather short, moderately broad and straight, arising near middle of gonapophysis in same plane as uncini on I and II (<i>kidderi</i>)	Short and very broad with tips obtuse, frequently curved downward, arising in distal third of gonapophysis, not in same plane as uncini on I and II (usually absent in <i>fairweatheri</i>)
Primary gonactinostal complex (adult male):	Broad; antero-posterior breadth about 1/3 to 2/5 length	Narrow; antero-posterior breadth about 1/4 length
Preorbital bone	More sculptured; with well-developed process projecting backward	Simple; roughly subtriangular in outline
Dorsal fin	More or less angulate; the free edge falcate	Rounded

nosta 2, 3 and 4 are distinctly separated in *Carlhubbsia*, in close apposition in *Phallichthys*; the anterior plate of bone on gonactinost 2 is broadly dilated or distended anteriorly in *Carlhubbsia*, only narrowly so in *Phallichthys*; and the posterior lateral wings on gonactinost 4 are accentuated in *Carlhubbsia*, only moderately developed in *Phallichthys*.

In summary, there are three principal differences between the suspensoria of *Carlhubbsia* and *Phallichthys*. In *Carlhubbsia* the uncini always originate along the proximal half of the shaft of a gonapophysis; in *Phallichthys* the uncini of gonapophysis I originate on the proximal half, but on gonapophyses II and III they originate on the distal half of the spine's shaft.

In *Carlhubbsia* the uncini are long, straight, and they merge with the gonapophyses rather abruptly; in *Phallichthys* the uncini are short, they are curvilinear, and they merge with the gonapophyses gradually, causing the spines to appear swollen at their tips. In *Carlhubbsia* the primary gonactinostal complex is greatly dilated anteroposteriorly; in *Phallichthys* it is relatively narrow.

Head Skeleton and Dentition

In both *Phallichthys* and *Carlhubbsia* the head skeleton is typical of such poeciliid species as *Poecilia vivipara* and *Xiphophorus maculatus* whose principal diet consists of organic debris, minute aquatic organisms and plant material. In both genera, the base of the cranium is high and firmly fixed in position by means of well-developed supraoccipital and epiotic processes, which join the high, expanded neural crests of the cervical vertebrae by means of strong ligaments. This type of deep, immobile skull is characteristic of other sluggish, forage-feeding fishes as well. Similarities in basic skull form in the two genera may as reasonably be interpreted to reflect similar feeding behavior as intimacy of relationship. The only superficially obvious skull differences occur in the orbital bones. In *Carlhubbsia* the preorbital (lacrymal) is more sculptured and has a well developed process produced backward toward the lateral ethmoid; in *Phallichthys* it is simple, roughly subtriangular in outline.

The dentigerous features of premaxillae and dentaries are similar in *Carlhubbsia* and in *Phallichthys*, although the shape of the inner bands is distinctive in *P. fairweatheri*. Such nutritional adaptations as tooth structure and size and orientation of dentigerous borders are notably variable in some poeciliid genera (e.g., *Poeciliopsis*), and the taxonomic usefulness of these characters is limited accordingly. To some degree, tooth structure varies independently of basic architecture of mouth parts. In *Carlhubbsia* and *Phallichthys*, for example, the jaws are weak, blunt and loosely joined at the midline. Yet *Phallichthys fairweatheri* has a broad, curved inner band of minute teeth and *P. amates* and the species of *Carlhubbsia* have a nearly straight, narrow inner band of longer teeth. Jaw structure is fundamentally similar in the poeciliid genera *Aulophallus*, *Quintana* and *Girardinus*. In *Aulophallus* the teeth of the outer series are setiform, in *Quintana* they are more or less conical and sharply pointed, and in *Girardinus* they are broadly oblanceolate. In general, it appears that in this family dental characters offer little hope of aiding phylogenetic analysis. Systematic ar-

rangements of the Poeciliidae and other cyprinodontiform groups based on these and other nutritional features have been subjected to just criticism (e.g., Hubbs & Turner, 1939; Miller, 1956).

Sensory Canals

Both *Carlhubbsia* and *Phallichthys* exhibit moderately well developed sensory canal systems, although problems in their direct comparison arise due to changes in the canals associated with size and age. Closed canals of large females may be represented only as open grooves in juveniles, in small adults, or even in mature males. Thus, of ten adult females of *Carlhubbsia kidderi* (UMMZ 144203) 28 to 34.5 mm. in standard length, the supraorbital canal is closed between pores 2 to 4 and 6 and 7 in nine, and from 2 to 3 and 6 to 7 in one, the smallest; the preopercular canal is closed and has 7 pores in eight, has 8 pores in one, and has 6 pores and a short groove in the smallest; and the preorbital canal has 3 pores in all. But of ten adult males from 16 to 20.5 mm. long from the same series, the supraorbital canal is developed from 2 to 4 and from 6 to 7 in six, from 2 to 3 and 6 to 7 in one, from 6 to 7 in one, and is represented only by grooves in two; the preopercular canal consists of 6 pores in seven, of 4 in two, and of 3 in one, the remaining portions being evidenced by open grooves; and the preorbital canal has 2 pores and a groove in three and consists of a groove only in seven. In *Carlhubbsia* and *Phallichthys* the mandibular canal is never developed, in the definitive condition the preopercular canal has 7 pores in all species, and the preorbital canal has 3 pores except for *C. stuarti* which has 4. The apparently definitive condition for the supraorbital canal is to have a tube with three pores above the eye (pores 2, 3 and 4a) and one with 2 behind it (pores 6 and 7) in all species. This arrangement is usually found in both species of *Carlhubbsia*, at least in adult females, and sometimes, especially in very large females, in the forms of *Phallichthys*. In most adults of *Phallichthys*, however, only the short postorbital section of the canal is covered. In three of ten adult females of *C. stuarti* examined, there is a third remnant of the supraorbital canal connecting pores 4b and 5.

In general, *Carlhubbsia* and *Phallichthys* are similar in the pattern of their sensory canals. But this pattern is essentially the same as that reported by Gosline (1949) for *Mollieniesia latipinna* and *Girardinus metallicus* and is close to that found in *Platypoecilus* (= *Xiphophorus*) *maculatus* and *Poeciliopsis* sp. We therefore find it impossible at this time to treat the simi-

larities in sensory canal pattern in *Carlhubbsia* and *Phallichthys* as indicative of a phylogenetic relationship.

RELATIONSHIPS OF *Phallichthys* AND STATUS OF THE POECILOPSINAE

Based chiefly on similar asymmetric modifications of the gonopodium of adult males, the genera *Phallichthys*, *Poeciliopsis*, *Poecilistes*, *Aulophallus*, *Xenophallus*, *Phalloptychus* and *Carlhubbsia* (as *Allophallus*) have been associated as a subfamily, the Poeciliopsinae, by Hubbs (1924, 1926, 1936). It has been inferentially suggested (Miller, 1955:50) that the monotypic genus *Poecilistes* is a generic synonym of *Poeciliopsis*. We find that the inner teeth in *Poecilistes pleurospilus* are much reduced in number, uniserial, and are restricted to the lateral ends of a row in each jaw. The supposed absence of the inner teeth has been employed as the primary basis for removal of *Poecilistes* from *Poeciliopsis* (Hubbs, 1936:233), a separation that can no longer be accepted. As a result of comparative morphological study we believe that the above association consists of four divisions, one comprising *Phallichthys*, *Poeciliopsis* and *Aulophallus*, the others *Phalloptychus*, *Xenophallus* and *Carlhubbsia* respectively. Each division is representative of what appears to constitute a distinctive phyletic line.

The diagnostic features of *Poeciliopsis* (see also Hubbs, 1936, and Hubbs & Miller, 1954) include: (1) body slender with posteriorly-placed dorsal fin; (2) gonopodium tightly rolled into a partially closed tube; ray 4p with paired, asymmetrical terminal retrorse serrae; terminal segments of ray 5 simple, without ornaments; rays 7 and 8 converging or in contact along middle of their lengths; (3) gonapophyses with uncini nearer distal than proximal end of shaft; uncini with broad bases and ventrally-arched, blunt tips; and (4) primary gonactinostal complex greatly dilated antero-posteriorly and deeply notched at dorsal margin, the incorporated shafts of actinosts 2, 3 and 4 flaring outward and upward away from the consolidated basal components.

With two exceptions, *Aulophallus* shares the above features with *Poeciliopsis*. It differs principally in the development of unpaired serrae on ray 4p of the gonopodium and in the transverse widening of terminal elements of ray 5a which in *Poeciliopsis* are greatly compressed. Dentition, used formerly to separate these groups, should be carefully reviewed, since within *Poeciliopsis* tooth form and orientation and size of the dental ridges are highly variable, according to Robert R. Miller (personal com-

munication—see also Hubbs, 1936: 235). The demonstrable intimacy of relationship between *Poeciliopsis* and *Aulophallus* may eventually necessitate their merger.

That the species of *Phallichthys* may have evolved directly from a form having symmetrical or nearly symmetrical gonopodial elements rather than from a *Poeciliopsis*-like fish, is suggested by the presence of only moderately incurved spinous processes on ray 3, the presence of a high, laterally compressed ridge on 4p and the lack of definitive closure of the groove at any point along the gonopodium. In the evolution of asymmetrical genitalia in Poeciliidae, formation of a fixed unilateral groove is made possible by folding of the rays, incurving of elements of ray 3 to form the ventral wall of the groove and compaction and superimposition of rays following loss of basic rotatory mechanisms (Rosen & Gordon, 1953). The segment ridge on ray 4p of the gonopodium in *Phallichthys* almost certainly is a remnant of the dorsal center of rotation (between rays 4 and 5) that is a constant feature of almost all symmetrical gonopodia. This, in turn, suggests that in *Phallichthys* some rotatory movements may occur during fin erection; additional mechanical adjustments would seem almost obligatory in order for the ray 5 complex to be apposed with the only moderately incurved spines of ray 3. The low degree of closure of the unilateral groove of the resting fin in both *P. fairweatheri* and *P. amates* contrasts sharply with the compact, twisted or even helical gonopodia in species of *Poeciliopsis*. In the latter forms, maximal folding of rays 3, 4 and 5 occurs during development, and no further positional adjustments accompany fin erection. The morphological differences separating these genera are summarized in Table 20.

Despite many differences in the details of their gonopodia and gonopodial suspensoria, *Phallichthys* and *Poeciliopsis* display a number of broad similarities. In their gonopodia we find: (1) segments on one-half of ray 3 rolled inward to form the ventral wall of the unilateral groove; (2) segments of ray 4a simple and without ornaments; those of 4p with a series of terminal retrorse serrae (paired though asymmetrical in *Poeciliopsis* and *Phallichthys fairweatheri*, unpaired in *Phallichthys amates* and *Aulophallus*); and (3) segments of ray 5 simple and much reduced. In their gonopodial suspensoria, we find: (4) uncini usually arising well out on gonapophyseal shaft; and (5) uncini with heavy bases, their tips blunt and developed in an arch downward. In view of over-all similarities in form and orientation of their male secondary

TABLE 20. COMPARISON OF *Phallichthys* AND *Poeciliopsis**

Character	<i>Phallichthys</i>	<i>Poeciliopsis</i>
Form	Body deep and compressed	Body slender and more terete
Body depth (percent. of standard length)	32 to 44	About 22 to 31
Body circumference scales	21 to 24	19 to 21
Dorsal origin (females)	Slightly in advance of anal origin	Decidedly behind anal origin
Dorsal rays	8 to 11; infrequently 8	Usually 7 or 8
Vertebrae	27 to 30, modally 28 or 29	29 to 33, modally 30 to 32
Suborbital dark bar	Present, more or less oblique; sometimes faint	Absent
Mandibular canal	Never developed	Often present; sometimes absent
Gonopodium:		
Form	Asymmetry less extreme; no definitive closure of groove	Twisted into a tightly rolled and partially closed tube
Spinous processes on ray 3	Moderately incurved	Strongly incurved
Subterminal segments of ray 3	Not consolidated	Usually several consolidated to form a slender rod
Ray 4p	With high laterally compressed ridge; terminal retrorse serrae paired or unpaired	Without high ridge; terminal retrorse serrae paired
Rays 7 and 8	Symmetrical; well separated at middle of their lengths	Distorted; converging or in contact at middle of their lengths
Suspensorium:		
Gonapophyseal uncini	Stout, broad-based, short, curved downward, usually emerging on distal half of spine; not lying in same plane	Stout, broad-based, usually short, curved downward, emerging on distal half of spine; not lying in same plane
Gonactinostal complex	Narrow antero-posteriorly; neither dilated nor notched at dorsal end	Dorsal end dilated antero-posteriorly and deeply notched

* Dr. Robert R. Miller is engaged in a revisionary study of *Poeciliopsis* which, when completed, will permit a much more adequate contrast of these genera.

sexual specializations, it is possible that *Phallichthys* and *Poeciliopsis*, with *Aulophallus*, may have radiated from a common prototype in which developmental patterns for gonopodial asymmetry were first becoming established. The difference in direction of gonopodial asymmetry of *Phallichthys fairweatheri* (dextral) and *P. amates* (sinistral) could have come into existence by means of a genetic "switch" mechanism that controlled direction of asymmetry at a critical point during epigenesis; it does not necessarily represent a fundamental divergence between these two species.

The Uruguayan genus *Phalloptychus* is characterized by having extremely well developed, projecting and more or less vertically oriented, unpaired serrae at the tip of gonopodial ray 4p, and long, straight and slender suspensorial uncini that emerge from the bases of and extend horizontally backward from gonapophyses II and III. With reference to their zoogeography

and comparative morphology, the two tiny species of this South American genus are highly distinctive. We find no basis for an alliance between this genus and the group including *Phallichthys*, *Poeciliopsis* and *Aulophallus*.

Similarly, the Central American *Xenophallus* has no special combination of gonopodial or suspensorial traits which, in our opinion, associate it with *Poeciliopsis* and its allies. The gonopodium (see Rosen & Gordon, 1953:29) is remarkably simple, without serrae or spines; it is specialized only in the sinistral or dextral folding and in the prolongation of the tip of ray 4a as a single, consolidated curved bony rod. In its suspensorium, uncini on gonapophyses I, II and III arise on the basal half of the gonapophyseal shafts along a single axis, and they are linear and rather slender. The relationships of both *Phalloptychus* and *Xenophallus* will be discussed more fully in a forthcoming publication (Rosen, ms.).

Evidence has been presented above suggesting that *Carlhubbsia* is not intimately related to *Phallichthys* or to any other member of the heterogeneous assemblage heretofore lumped as the subfamily Poeciliopsinae. Nowhere in the group are there other forms having suspensorial and gonopodial details like those of *Carlhubbsia*. Among the remaining major groups of poeciliids we find a constellation of features which most closely resembles those of *Carlhubbsia* in the endemic Cuban genera *Quintana* and *Girardinus* (see below, pp. 35-39).

From a functional standpoint it may seem elementary to suggest that asymmetric folding of the primary anal rays to form a permanent closed or partially closed tube would produce a highly adapted vehicle for sperm transfer. All poeciliid fishes not so equipped create a transitory tube by folding the anal rays at each copulatory attempt. Thus all members of this group, and indeed others that similarly employ the anal fin to effect internal fertilization, are in a sense preadapted to the evolution of a permanently asymmetric genitalium. Permanent folding permits structural modification to enhance the effectiveness of the mechanism. That a development so useful in the maintenance of species should evolve but once in this family in which gonopodial plasticity is abundantly demonstrated is conceivable, but a polyphyletic origin of asymmetry is certainly to be anticipated.

Justification for dismemberment of the Poeciliopsinae rests solidly with the weight of evidence from study of the fine details of the gonopodium (apart from its asymmetry) and gonopodial suspensorium. Gonopodial asymmetry, far from being a uniting character, almost certainly has appeared independently at least five times within the Poeciliidae [in *Phallichthys*-*Poeciliopsis*-*Aulophallus*, *Phalloptychus*, *Xenophallus*, *Carlhubbsia* and in *Xenodexia ctenolepis*, regarded by Hubbs (1950) as constituting a distinct subfamily], and in two other cyprinodontiform families, the Jenynsiidae and Anablepidae. The beginnings of such a pattern can be seen in still another poeciliid genus, *Quintana*, in which serrae on ray 4p of the gonopodium are always twisted sinistrally.⁴

⁴ C. L. Hubbs (Occ. Pap. Mus. Zool., Univ. Mich., 302: 1-3, 1935), in an article entitled "Studies of the fishes of the Order Cyprinodontes. XIV. *Plectrophallus* regarded as a distinct genus," figured the gonopodium of the poeciliid *Plectrophallus tristani* (Fowler) to illustrate the asymmetric folding of the rays. This would, of course, represent yet another example of the independent origin of asymmetry in the family, since *P. tristani* is probably allied to the species of *Brachyrhaphis*. *P. tristani* is known from but one specimen, however, and we have not seen this.

Carlhubbsia AND THE CUBAN ENDEMIC POECILIIDS

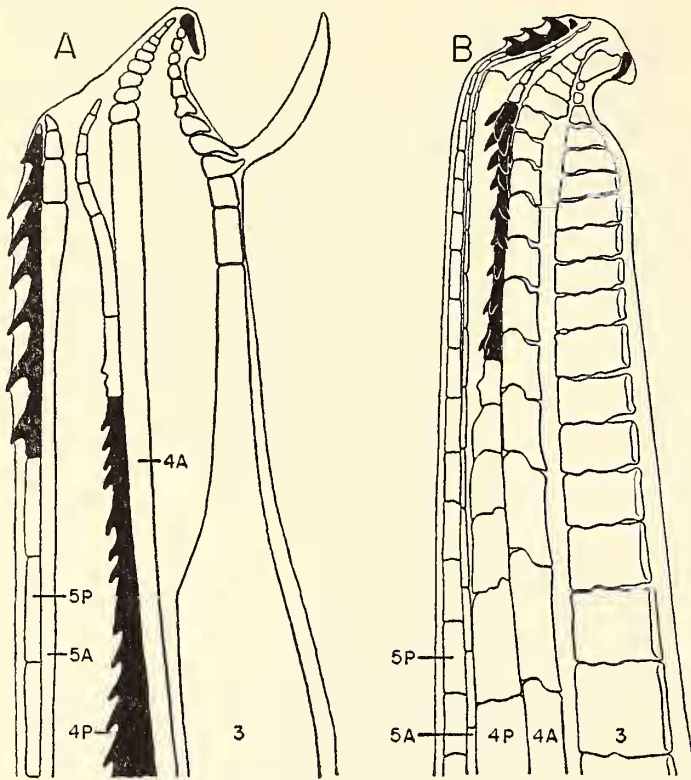
Our attempt to decipher the relationships of *Carlhubbsia* has led us to investigate the Cuban poeciliids which in current classification constitute the tribes Girardinini and Quintanini. Howell Rivero & Rivas (1944) called attention to the integrity of the girardinini, and pointed to the distinctiveness and uniformity of their gonopodia and suspensoria. Suspensorial structures were studied further by Howell Rivero (1946) and the compactness of the Girardinini was again emphasized. This group, now numbering about 10 recognized species, was arranged in five genera that were separated chiefly on the basis of dentition and mouth structure. There are at most minor differences, mostly average features, in the gonopodia of all groups except *Toxus*, which, though sharing the prominent horn-like terminal appendages and all specialized bony structures, has the most distinctive gonopodium of the five genera. Howell Rivero & Rivas (1944: 14) summarized their study of these fishes as follows:

"In their fundamental features, therefore, the genera of the Girardinini are in almost complete agreement. The radiative adaptation of these genera seems to have been related chiefly to food habits, for most of the generic characters involve the structure of the jaws, mouth and teeth (see key to genera). There is every reason to believe that the genera of the tribe have evolved in Cuba, after a single ancestral species migrated into what is now that island."

As mentioned above, dentitional characters have been seriously over-emphasized in the systematics of the cyprinodontiform fishes. The gonopodia and suspensoria of the girardinini fishes (Howell Rivero & Rivas, 1944; Howell Rivero, 1946; Rosen & Gordon, 1953: 27) show numerous and striking similarities. This is so manifestly a compact group phylogenetically and zoogeographically that we prefer to classify the species in a single genus, *Girardinus* Poey, of which *Glaridichthys* Garman (including *Glaridodon* Garman), *Toxus* Eigenmann, *Dactylophallus* Howell Rivero & Rivas and *Allodontium* Howell Rivero & Rivas are generic synonyms. Thus, *Girardinus* as amended is equivalent to the Girardinini of recent authors. Since *Quintana* is the only genus in the tribe Quintanini, these terms also are equivalent in scope.

Girardinus and *Quintana*

That *Quintana atrizona* is highly distinctive was clearly indicated by Hubbs (1934) in the original account. He placed the genus in the



TEXT-FIG. 7. Distal tips of the gonopodia of: A. *Girardinus denticulatus* (Garman), and B. *Quintana atrizona* Hubbs, as seen from the left side. Bony elements being compared are shown in solid black.

subfamily Gambusiinae and, hesitantly, in the tribe Heterandriini. Certain similarities to *Gambusia*, *Allogambusia* and *Girardinus* (*sensu lato*) he regarded as more plausibly due to parallelism and convergence than to common origin. Howell Rivero & Rivas (1944: 13) granted separate tribal status to *Quintana*, but commented that "Our continued studies have emphasized the integrity of the Cuban group Girardinini, although the gonopodial characters of *Quintana* (see key) somewhat confuse our views as to the isolated position of this group." Howell Rivero's description and figure of the suspensorial apparatus of *Quintana* (1946) clearly indicate the unique features. He reported that only the second of the three gonapophyses is appreciably specialized and complex, an observation not fully substantiated by our material.

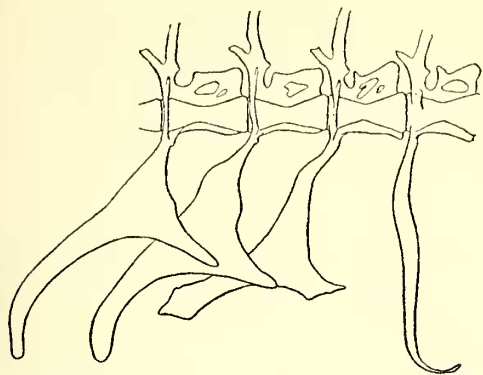
Recent evidence has been found to support the hypothesis that *Quintana* and *Girardinus* arose on Cuba from invasions of a single or of two closely related forms (Rosen, ms.). If this is true the affinities of these genera should be emphasized by their close association in the systematic structure of the family. For the present purposes it is sufficient to note certain structural similarities.

In the gonopodia and gonopodial suspensoria

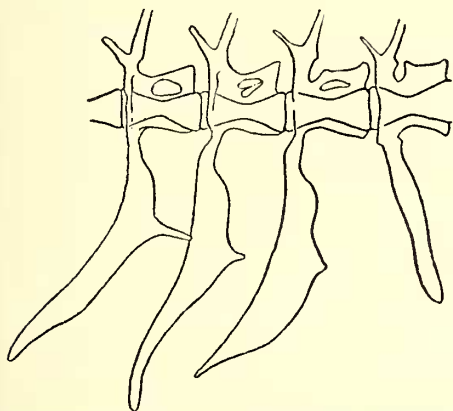
of *Quintana* and *Girardinus* (Text-figs. 7, 8 and 9), we find the following diagnostic structures that we interpret as homologous in these genera: (1) a minute, recurved, terminal hook on ray 3; (2) weak retrorse serrae on ray 4p; (3) moderately to well-developed serrae on ray 5p; (4) three highly specialized gonapophyses; and (5) uncini developed on all three gonapophyses. To these may be added similarities of body form and fin shape. All species are streamlined, all have the dorsal and ventral trunk profiles symmetrically arched, and in all the caudal peduncle is long and slender. The median fins, particularly the dorsal, tend to be sharply pointed and even falcate.

Characters Indicating Relationship of Carlhubsia with Quintana and Girardinus

If we deal first with the primary terminal specializations on rays 3, 4 and 5 of the gonopodium (Text-fig. 10) and allow for the minor modifications which are probably to be attributed to asymmetric growth, we find that with but one important exception the gonopodia of *Quintana* and *Carlhubsia* are much alike. They share the following similarities: in ray 3 both have a series of stout proximal elements that become considerably compressed apico-basally



TEXT-FIG. 8. Axial division of the gonopodial suspensorium of *Girardinus creolus* (Eigenmann), showing the three gonapophyses and a slightly modified hemal spine. Anterior to the left.



TEXT-FIG. 9. Axial division of the gonopodial suspensorium of *Quintana atrizona* Hubbs, showing the three gonapophyses and a slightly modified hemal spine. Anterior to the left.

towards the tip of the ray. At the exposed margin of the ray about ten terminal segments that are decidedly higher than long are produced into broad, flat spines; the most distal extent of the posterior spinous processes contribute to the formation of the eccentric groove that arises obliquely from the ventral margin of this ray. In *Carlhubbsia* the single, dextral eccentric groove forms the permanent anterior edge of the partially folded gonopodium. In *Quintana* the eccentric grooves on both sides of the ray serve as the anterior edge of the transitory channel when the gonopodium is swung forward and to one side during fin erection (Rosen & Gordon, 1953: 18-23). In both, ray 3 is terminated by an abruptly widened, segmented or consolidated, bony complex and by a minute recurved bony hook (in *C. stuarti*, the hook is replaced by an uncalcified though rigid membranous structure). In both *Carlhubbsia* and *Quintana* ray 4a is

slender proximally and abruptly shortened and widened distally. Ray 4p in both genera is slender distally (usually obsolescent in *Carlhubbsia*) and bears a cluster of retrorse serrae. These serrae are rotated sinistrally in both genera. Ray 5p in both *Quintana* and *Carlhubbsia* is terminated by a series of erect though short serrae. The subdistal segments of ray 5a, which in *Quintana* develop as an "elbow-like" structure, and the profound asymmetry in *Carlhubbsia* are the only gonopodial features in which the two groups differ significantly.

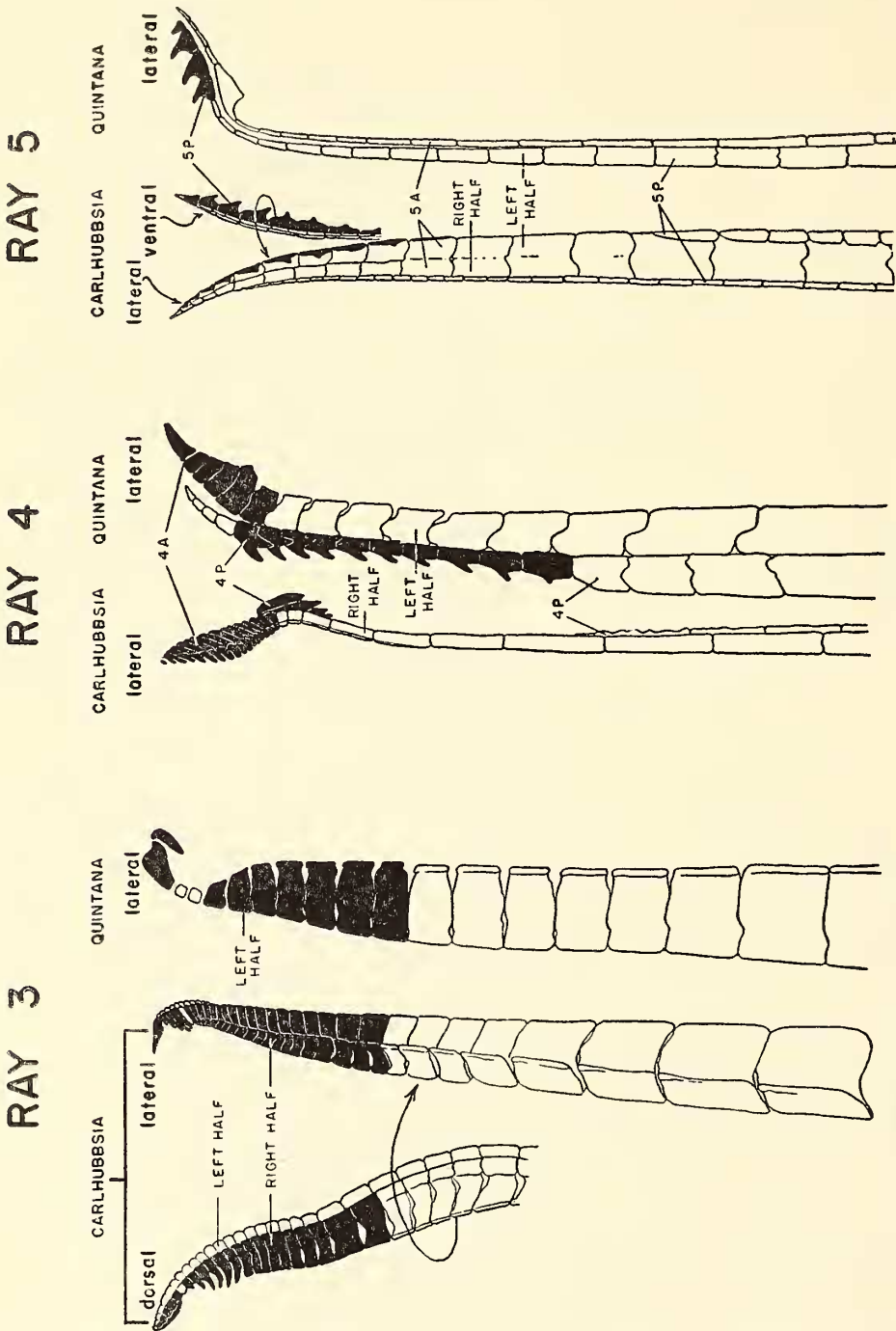
In the gonopodium of *Girardinus*, ray 4a is not expanded distally, the spines of ray 3 are smaller, less numerous, and are delicately pointed, and a conspicuous pair of fleshy subradial processes originates below the spines of ray 3 and extends in an arc forward and laterally.

Of all the taxonomically significant morphological details, those of the gonopodial suspensorium show the most striking similarities among the species of *Carlhubbsia*, *Quintana* and *Girardinus* (Text-figs. 5, 8 and 9). In each, the three gonapophyses all bear uncinatoid processes that lie more or less in the same plane at an angle of approximately 30° with the vertebral axis. The uncini in all are limited to the proximal portion of the spine's shaft, and are always linear, pointed and rather slender.

The gonapophyses of the suspensorium of *Quintana* were described and figured by Howell Rivero (1946) as being simple and having but a single pair of uncini. Actually the suspensorium of a paratype of *Q. atrizona* (Text-fig. 9) shows small uncini on all three gonapophyses. *Quintana* and *Girardinus* are considerably more alike than had been thought from earlier studies. In suspensorial structure they differ only in the extent of development of the uncini; in *Girardinus* (as well as in *Carlhubbsia*) the uncini are relatively large, strongly produced, and overlapping. Howell Rivero's Figure 10, which shows almost complete lack of specialization of gonapophyses I and II of *Quintana*, indicates that he may have worked with subadult males in which the fine details of suspensorial structure had not yet fully developed.

Résumé of Morphological Analysis and Conclusions

Since the similarities in certain skeletal features in *Carlhubbsia*, *Quintana* and *Girardinus* are not always clearly defined and the alleged homologies may seem questionable, it may be contended that many or all of the resemblances are examples of evolutionary parallelism. It is



TEXT-FIG. 10. Comparison of the disarticulated principal gonopodial rays of *Carlhubbsia kielderi* (Hubbs) and *Quintana atrizona* Hubbs. The individual rays are oriented as in the articulated gonopodium when viewed laterally. Rays 3, 4, and 5 of *Carlhubbsia* are viewed from the right, those of *Quintana* from the left, in order to reveal the maximum number of details. The compared elements are in solid black. An additional view of ray 3 of *Carlhubbsia* shows the tip of this ray in dorsal view after it has been rotated 90° to the left. The additional view of ray 5 of *Carlhubbsia* shows the tip of this ray in ventral view after it has been rotated 90° to the right. Curved arrows indicate direction of rotation necessary to bring these back to the normal (lateral) position.

often possible, however, to recognize the existence of spurious similarities that define an adaptive trend in gonopodial and suspensorial structure, and at the same time to recognize evidence for homology where it exists. Considering the totality of morphological evidence for the similarities between *Quintana* and *Girardinus*, we

regard as homologous the distal serrae (ray 5p), the proximal serrae (ray 4p) and the terminal hooks (ray 3) in their gonopodia. The spines (ray 3), however, may have developmentally different origins because in *Girardinus* the spines are always intimately associated with large fleshy ventral processes, structures that are altogether

wanting in the gonopodium of *Quintana* (Text-fig. 7). In both groups the presence of spines on ray 3 (irrespective of their developmental origins) is undoubtedly related to a specialization of segments for sensory function (see Rosen & Gordon, 1953).

When we consider the sum of the morphological evidence it is apparent that the resemblances among *Carluhubbsia*, *Quintana* and *Girardinus* are mosaic. For example, the suspensorium in *C. kidderi* most closely resembles that of *Girardinus*, less so that of *Quintana*, and least of all that of its congener *C. stuarti*. The gonopodium of *C. kidderi*, on the other hand, most closely approximates that of *C. stuarti*, less so but still significantly that of *Quintana*, and least of all that of *Girardinus*. A consideration of general body form and fin structure suggests additional complex interrelations, for among the recognized species of *Girardinus* there is no well established norm that can be defined precisely. In *Girardinus creolus*, for example, the contours are quite flat whereas in *G. falcatus* and *G. uninotatus* they are sharply angulated. Again, in *G. creolus*, the mouth is distinctly terminal whereas in *G. cubensis* and *G. denticulatus* it is superior; the latter two have previously been separated generically on the basis of further differences in the structure of the mouth parts and position of the gape. In *G. falcatus* the median fins are sharply pointed, whereas in *G. creolus* they are distinctly rounded. In *Quintana* the contours are sharply angulated; in *Carluhubbsia stuarti* the body contours may be so high as to be distinctly rhombic.

But despite the complexity of the many morphological interrelations there is evidence of a central theme. *Carluhubbsia*, *Quintana* and *Girardinus* have in common the following groups of characters in the gonopodium and gonopodial suspensorium:

- (1) a minute recurved terminal hook on ray 3;
- (2) spines on ray 3;
- (3) weak retrorse serrae on ray 4p;
- (4) moderately to well-developed serrae on ray 5p;
- (5) three highly specialized gonapophyses;
- (6) uncini almost always present on all three gonapophyses;
- (7) uncini all lying in same plane;
- (8) uncini always limited to the proximal portion of the spine's shaft; and
- (9) distal tips of gonapophyses I and II bent downward to meet the projecting actinosts below.

With recent knowledge of skeletal form and function in the Poeciliidae, primary emphasis is shifted from attention to slight differences in structure to the more significant basic similarities. The array of fundamentally distinctive morphological traits that are shared by *Car-*

hubbsia, *Quintana* and *Girardinus* constitutes strong presumptive evidence of their community of descent.

Zoogeographic Considerations

If *Carluhubbsia*, *Quintana* and *Girardinus* form a natural group, as is suggested above, then it seems plausible that a common ancestor of these fishes may have evolved from other poeciliid groups in the Atlantic coastal drainages of middle or southern Central America. Invasion of the Greater Antillean islands by a representative stock, by whatever means (possibly some form of waif dispersal), may have occurred as a result of coastal, northward spread on the mainland toward the Yucatan Peninsula. Myers (1938: 359) commented that *Girardinus* is distantly related to Central American types, and must have arisen in Cuba a long time ago. Verification of affinities of *Quintana* and *Girardinus* with the mainland *Carluhubbsia* strengthens the hypothesis that Central America served as the source from which the ancestors of *Quintana* and *Girardinus* made their way to Cuba. We concur with Myers' estimate that the Cuban forms have long been isolated. Although not now clearly demonstrable, the natural group composed of, or including, *Carluhubbsia*, *Quintana* and *Girardinus* may well have had its genesis in Central America. The geologic and zoogeographic evidence favoring Central America as one of the sources of the Antillean biota has been summarized recently by Darlington (1957).

The West Indian Poeciliidae may be divided into two major groups on the basis of their degree of morphological differentiation from the closest mainland relatives. One of these proves to be a natural grouping, the other artificial.

Group I. *Quintana* and *Girardinus* form a compact natural group. They are distinct generically from all known mainland forms. They occur naturally only on Cuba and the Isle of Pines. *Quintana* is monotypic. *Girardinus* is polytypic, with perhaps 10 species.

Group II. The tribes Poeciliini and Gambusiini recognized in current classification are placed in distinct subfamilies and they are not closely related. Zoogeographically, however, they have many points in common. On the mainland, the Gambusiini occur throughout southern North America and Middle America together with the Poeciliini; the latter in addition have spread across northern South America. In the West Indies the Poeciliini occur naturally in the Greater and Lesser Antilles and on islands off the coast of Nicaragua. Of

the eight genera currently recognized, five certainly occur in, and two, *Limia* and *Curtipenis*, are restricted to, the West Indies. All of the poeciliid genera are closely related, however, and they are only doubtfully distinct. The Gambusiini consist of two or three genera, of which *Gambusia* is widely distributed on the mainland and in the West Indies. In the West Indies *Gambusia* occurs chiefly in the Greater Antilles and in the Bahamas; one species is found on the coastal islands of Nicaragua; another, closely allied to a Cuban form, inhabits the Florida Keys.

In summary, *Quintana* and *Girardinus* are morphologically distinct from all poeciliid genera on the mainland; they are endemic to Cuba and the Isle of Pines. In the Gambusiini and Poeciliini, only two nominal genera are peculiar to the West Indies and these are closely related to widely distributed mainland forms.

The endemism and morphological distinctiveness of *Quintana* and *Girardinus* suggest that they have been derived from one or two early invasions of the West Indies from Central America. In contrast, the less marked differentiation of the West Indian poeciliids and gambusiids and their more general distribution through the Antilles and small coastal islands indicates that they are probably more recent additions to the Antillean fauna. The Gambusiini and Poeciliini probably penetrated the West Indies from Central America, the Poeciliini also from South America, at least into the Windward Islands (Myers, 1938).

SUMMARY

The genus *Carlhubbsia* Whitley contains two known species, *C. kidderi* (Hubbs), from Campeche, Mexico, and El Petén, Guatemala, and *C. stuarti*, n. sp., from the Río Polochic, Guatemala. The genus *Phallichthys* contains three recognized forms, two of which are provisionally ranked as subspecies: *P. amates pittieri* (Meek) from Panama and Costa Rica, *P. a. amates* (Miller) from Honduras and eastern Guatemala, and *P. fairweatheri*, n. sp., from El Petén, Guatemala, and British Honduras. Spot-distribution maps are given for all species: of the two genera only *Carlhubbsia kidderi* and *Phallichthys fairweatheri* are sympatric.

Although there is marked superficial resemblance among the species, it is contended that the two genera represent well separated phyletic lines and owe many common characters, including the asymmetrically folded external genitalia (gonopodia), to parallelism. In morphological assessment, it is noted that certain common features associated with permanent folding of

the gonopodium and with the configuration and orientation of the gonapophyses in the gonopodial suspensorium are highly adaptive, and have developed independently in the two lines. More fundamental, presumably antecedent, characters associated with the specialized terminal structures of the gonopodium, the positional relationships and form of the suspensorial uncini and the shape of the gonactinostal complex are interpreted as indicative of the true relationships.

In the species of *Carlhubbsia* and *Phallichthys* dentition is surprisingly uniform. Notable differences among closely related species within other poeciliid groups such as *Poeciliopsis* and *Girardinus*, however, indicate a highly adaptive plasticity and suggest that in this family less weight should be placed on denticular characters than formerly. In line with the above reasoning *Poecilistes* Hubbs is considered a synonym of *Poeciliopsis* Regan, and in view of notable similarities in basic pattern of gonopodial and suspensorial structures in the group previously called the Girardinini, we propose the reduction of *Glaridichthys* Garman (including *Glaridodon* Garman), *Toxus* Eigenmann, *Dactylophallus* Howell Rivero & Rivas, and *Allodontium* Howell Rivero & Rivas to the synonymy of *Girardinus* Poey. The latter name becomes equivalent to Girardinini, and *Quintana* is similarly of equal scope to Quintanini. There appears, therefore, to be no further necessity for retaining these tribe names, at least with their current limits.

In *Poeciliopsis*, *Aulophallus* and *Phallichthys*, the basic ornamentation of the gonopodium is relatively little specialized, although infolding, twisting and consolidation of the structure has proceeded further in *Poeciliopsis* and *Aulophallus* than in *Phallichthys*. Thus the latter genus is set somewhat apart from the others. It is suggested nevertheless that they constitute a natural group which may have arisen from an ancestor in which developmental patterns for gonopodial asymmetry were first becoming established. Since *Phallichthys* contains one species with the gonopodium dextral and one species with it sinistral, and because asymmetry is only moderately developed, it seems likely that the beginnings of this genus, as here defined, predate the time of origin of gonopodial asymmetry in the group as a whole. It is conceded, however, that the specific asymmetric modifications also may well have been independently derived in *Phallichthys*, and *Poeciliopsis* and *Aulophallus*.

In view of the lack of unifying structural bonds among *Phalloptychus*, *Xenophallus* and *Carlhubbsia*, or between any of these and the

group containing *Phallichthys*, *Aulophallus* and *Poeciliopsis*, other than that of a folded gonopodium, it is concluded that the Poeciliopsinae, defined on the basis of this character, is an artificial assemblage and should be disrupted.

Carlhubbsia, no longer regarded as closely related to *Phallichthys*, is shown to share many common features of the gonopodium and the suspensorium with the Cuban genera *Quintana* and *Girardinus*. Although these three seem properly separated at the generic level they form a natural group in the family. Thus, *Carlhubbsia* provides mainland representation of the Antillean group, and points to the probability that the ancestors of the Cuban genera came from Middle America. Such ancestors probably had symmetrical gonopodia, since those of *Girardinus* are symmetrical; in *Quintana* only a few segments near the tip are slightly twisted sinistrally. These genera are notably more sharply differentiated from *Carlhubbsia* than are other Antillean poeciliids from their mainland relatives. This suggests the likelihood that *Quintana* and *Girardinus* stem from an earlier invasion of the islands than do the poeciliins and gambusiins that live there.

ACKNOWLEDGMENTS

This attempt to advance our knowledge of *Carlhubbsia* and *Phallichthys* would have been fruitless except for the wealth of new and unreported collections of four of the five recognized forms. We deeply appreciate the privilege of studying these materials and for their contribution thank the collectors: the Rev. Gerald Fairweather, Drs. Myron Gordon, Carl L. Hubbs, Henry van der Schalie and Laurence C. Stuart. Most of the previously known specimens of these genera have been available on loan. We acknowledge the cooperation of Loren P. Woods, Chicago Natural History Museum, and of Drs. Leonard P. Schultz and Ernest A. Lachner, United States National Museum.

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The maps and Text-fig. 6 were prepared by Mrs. Elizabeth Anthony, and the photographs

were taken by William L. Brudon, both on the staff of the University of Michigan Museum of Zoology. Some of the X-rays and the prints made from them were prepared by Elwood Logan of the American Museum of Natural History. We thank all of them.

ADDENDUM

While the present manuscript was in press, there appeared in the Proceedings of the American Philosophical Society (102 [3]: 281-320, 1958) an article by L. R. Rivas entitled "The origin, evolution, dispersal, and geographical distribution of the Cuban poeciliid fishes of the Tribe Girardinini." Based on our independent morphological studies, we find that our views are at variance with those of Rivas in questions of the origin, relationships and taxonomy of the Cuban endemic poeciliids. We maintain without emendation our original interpretations. For further discussion of the zoogeographic problems the reader is referred to the recent reviews of W. P. Woodring (Bull. Geol. Soc. Amer., 65: 719-732, 1954), "Caribbean land and sea through the ages," and Darlington (1957).

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EXPLANATION OF THE PLATES

PLATE I

Carlhubbsia stuarti, n. sp., Río Polochic, near Panzos, Guatemala.

- FIG. 1. Holotype, UMMZ 146084, an adult male 38.3 mm. in standard length.
 FIG. 2. Allotype, UMMZ 172455, an adult female 50.5 mm. long. Photographs by William L. Brudon.

PLATE II

Carlhubbsia kidderi (Hubbs), Arroyo Subín, tributary to Río de la Pasión, El Petén, Guatemala (UMMZ 144217).

- FIG. 3. Adult male, 21.0 mm. in standard length.
 FIG. 4. Adult female, 36.5 mm. long. Retouched photographs by William L. Brudon.

PLATE III

Phallichthys amates pittieri (Meek), Siquirres, Limón, Costa Rica (USNM 92158).

- FIG. 5. Adult male, 23.5 mm. in standard length.
 FIG. 6. Adult female, 30.5 mm. long. Photographs by William L. Brudon.

PLATE IV

Phallichthys amates amates (Miller), tributary to Río San Alejo, San Alejo, Atlantida, Honduras (UMMZ 173221).

- FIG. 7. Adult male, 25.5 mm. in standard length.

- FIG. 8. Adult female, 32.0 mm. long. Photographs by William L. Brudon.

PLATE V

Phallichthys fairweatheri, n. sp., Río San Pedro de Mártir, El Petén, Guatemala.

- FIG. 9. Holotype, UMMZ 172456, an adult male 29.7 mm. in standard length.
 FIG. 10. Allotype, UMMZ 172457, an adult female, 33.3 mm. long. Photographs by William L. Brudon.

PLATE VI

- FIG. 11, A-F. Radiographs of the gonopodial suspensoria of six adult males of *Phallichthys fairweatheri*, n. sp. (UMMZ 144186), showing variability in form, orientation, and development of various structures. The gonactinostal complex is typically slender in A and B, somewhat less so in E and F, and unusually broad in C and D. The dorsal tip of the ligastyle lies beneath the 10th vertebra in A, D and E, and between the 10th and 11th vertebrae in B, C and F. Uncini near the base of gonapophysis I are typically well developed in A-D, small in E, and absent in F. Uncini near the tip of gonapophysis III are poorly developed or obsolescent in A and D-F, well developed in B and C.

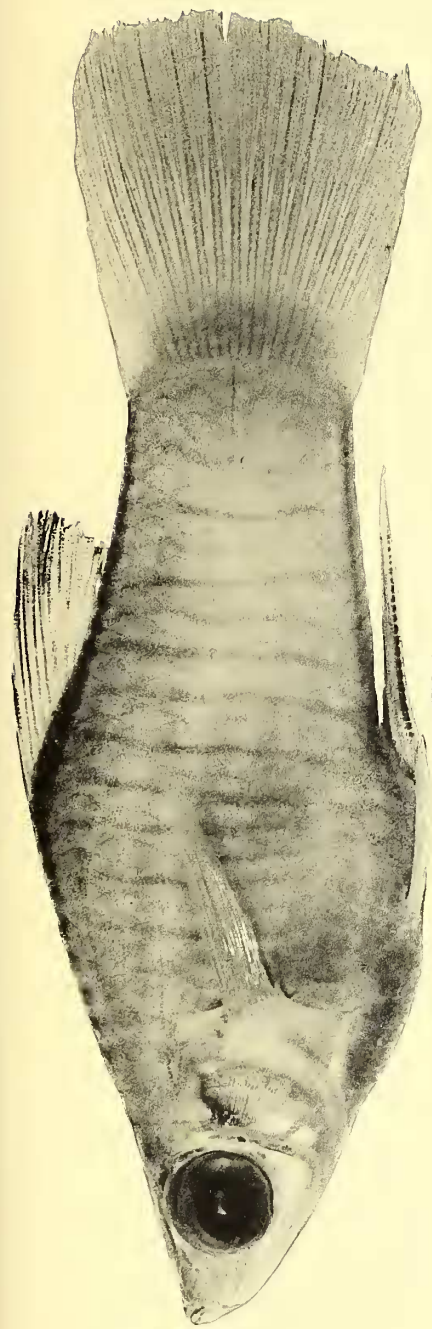


FIG. 1

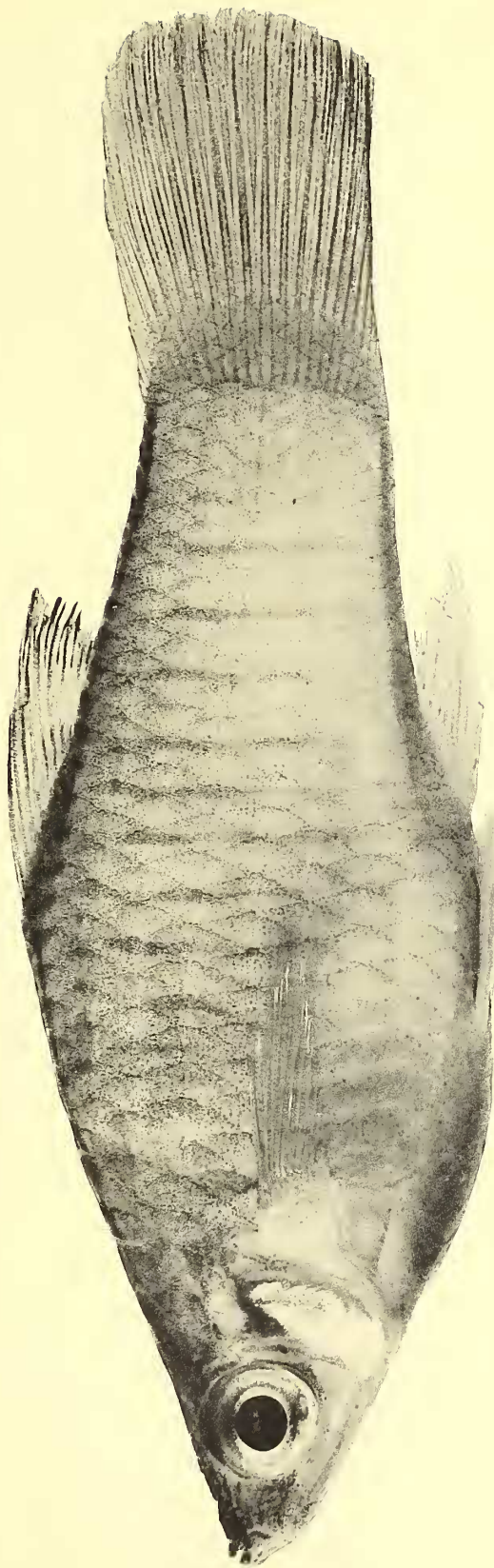


FIG. 2

MIDDLE-AMERICAN POECILIID FISHES OF THE GENERA CARLHUBBSIA AND PHALlichthys, WITH DESCRIPTIONS OF TWO NEW SPECIES

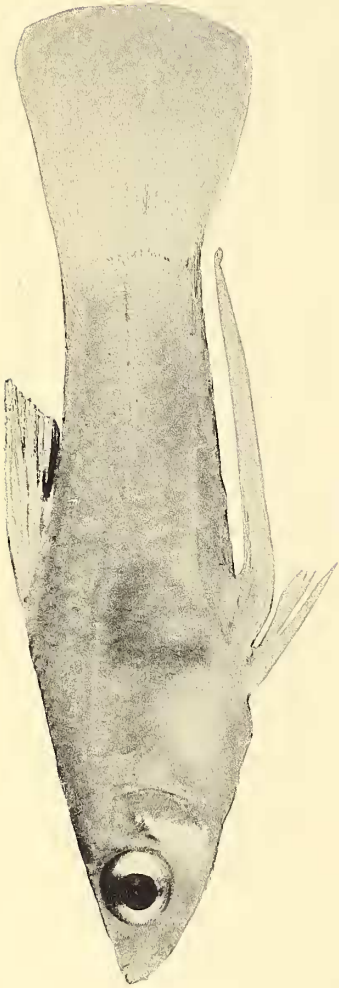


FIG. 3

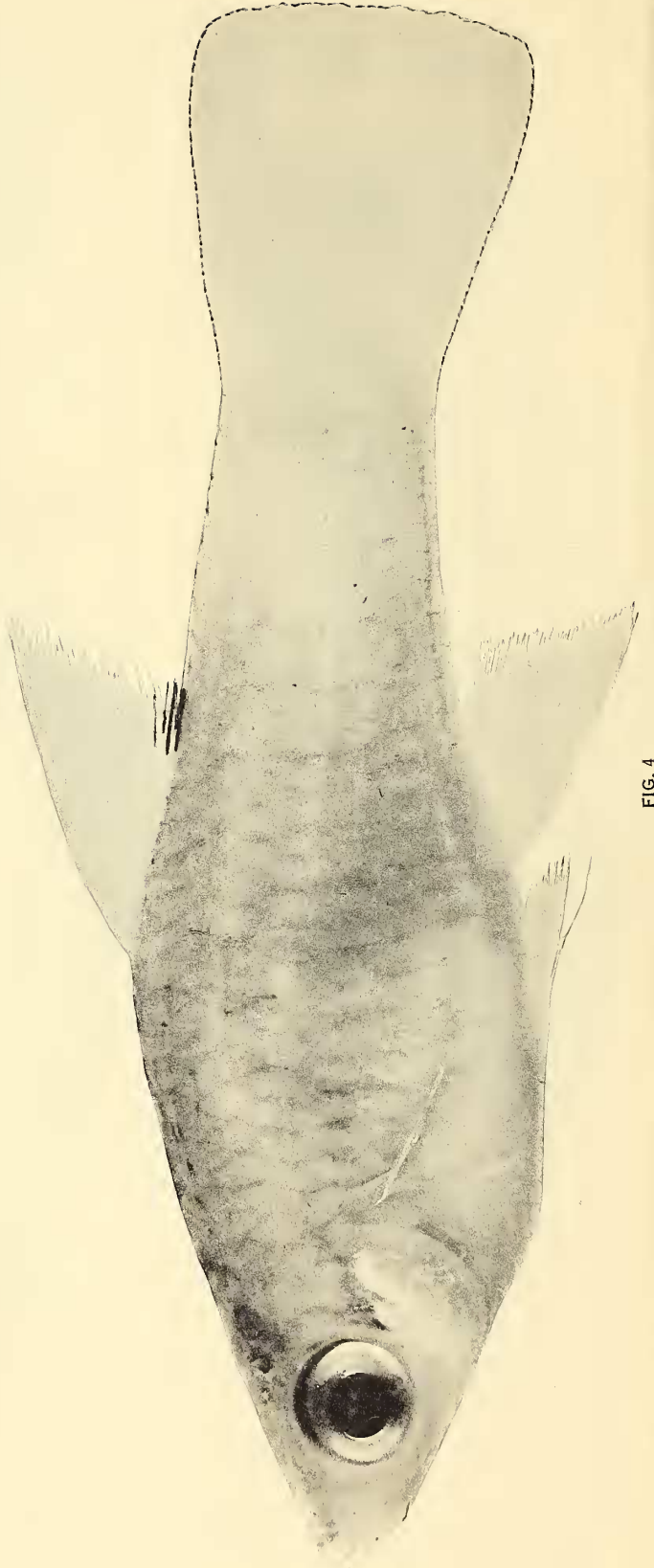


FIG. 4

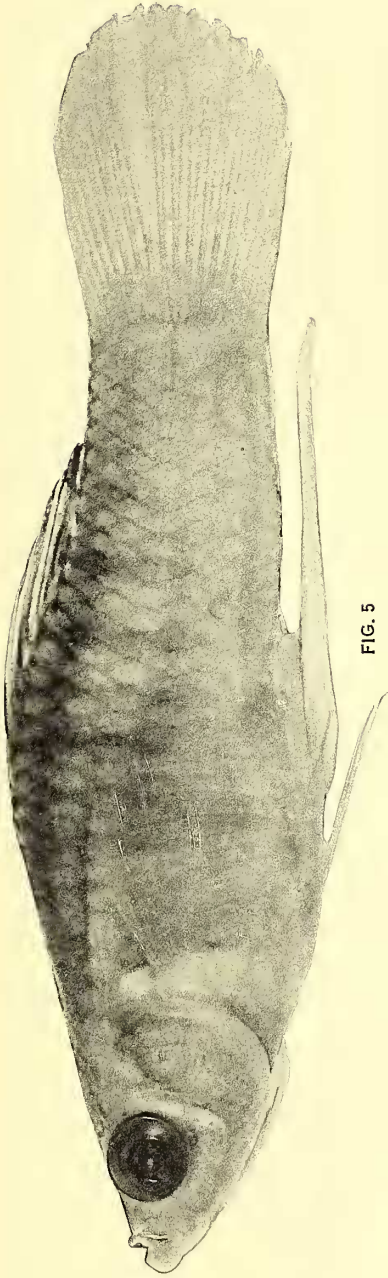


FIG. 5

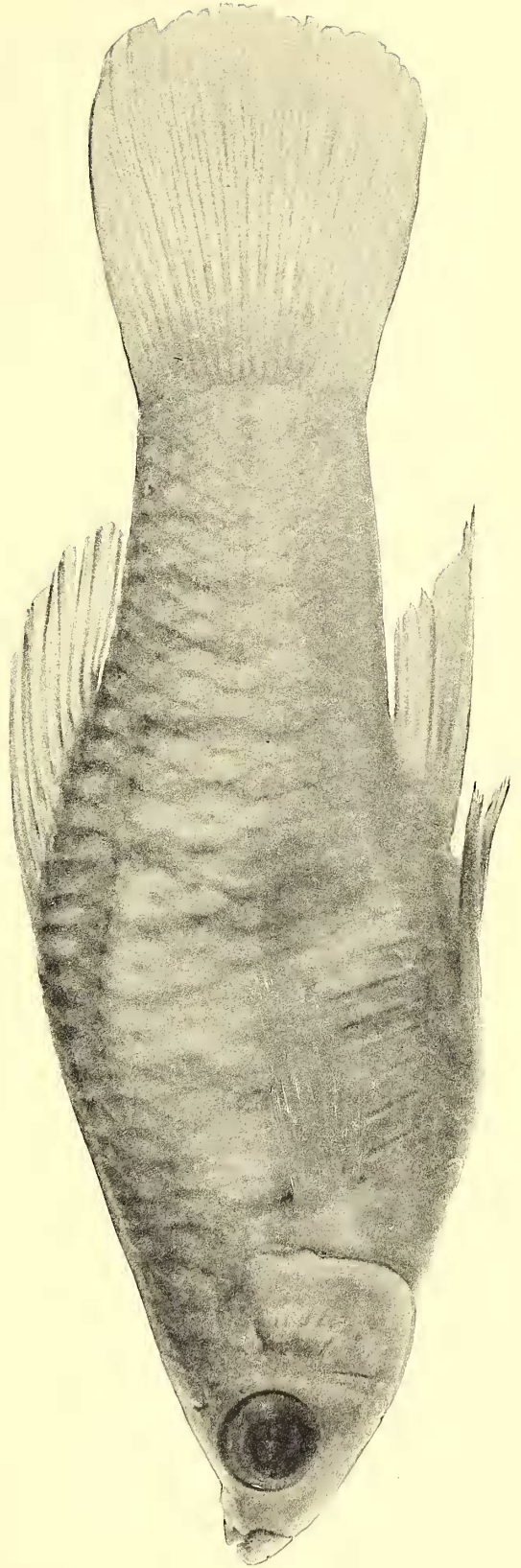


FIG. 6

MIDDLE-AMERICAN POECILIID FISHES OF THE GENERA CARLHUBBSIA AND PHALLICHTHYS, WITH DESCRIPTIONS OF TWO NEW SPECIES



FIG. 7

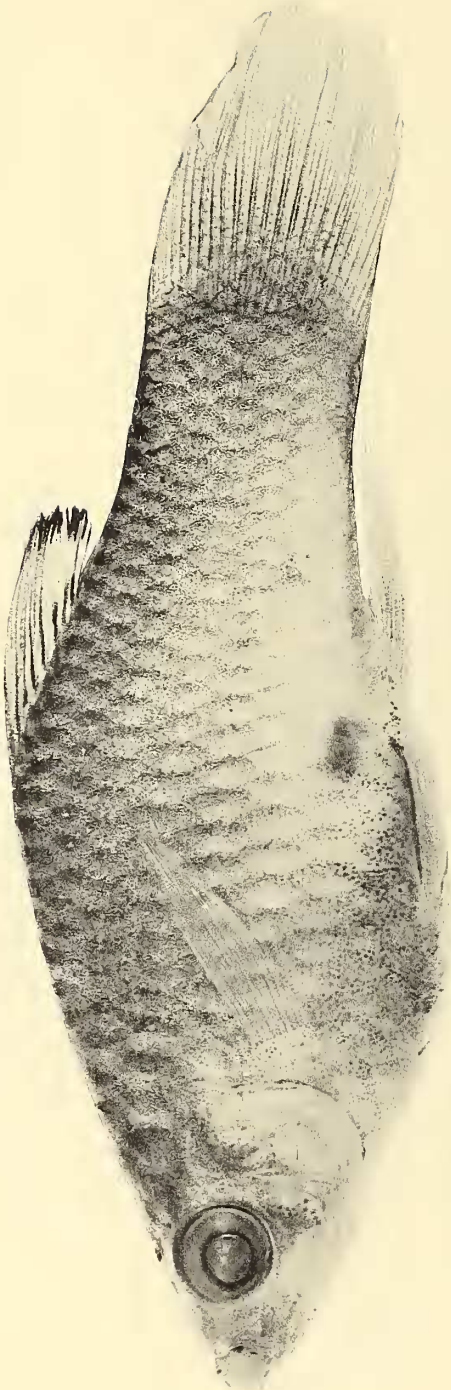


FIG. 8

MIDDLE-AMERICAN POECILIID FISHES OF THE GENERA CARLHUBBSIA AND PHALLICHTHYS, WITH DESCRIPTIONS OF TWO NEW SPECIES

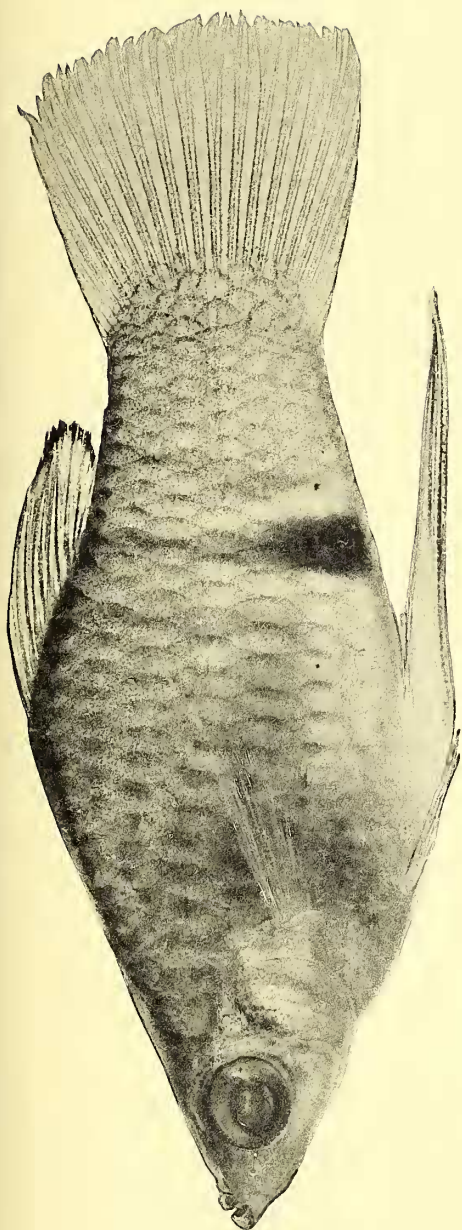


FIG. 9

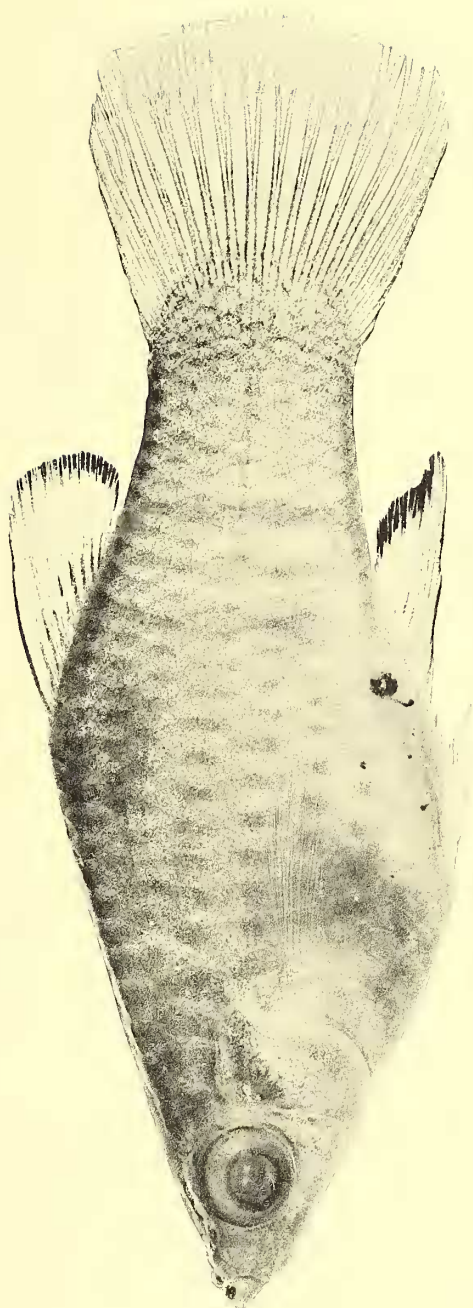
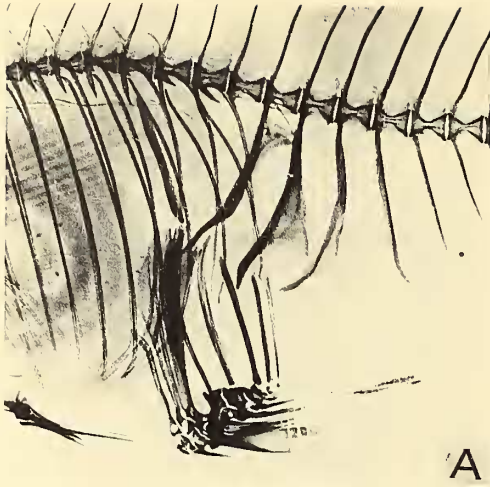
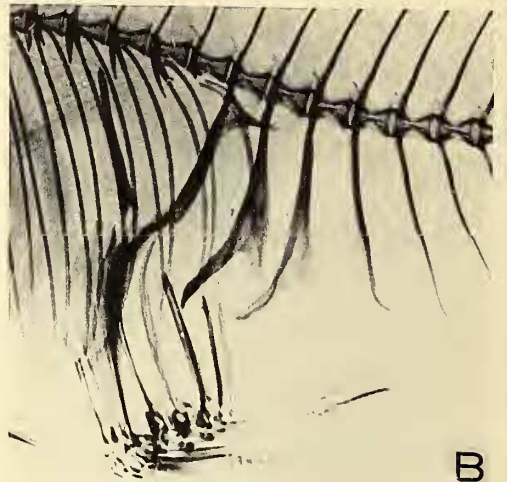


FIG. 10

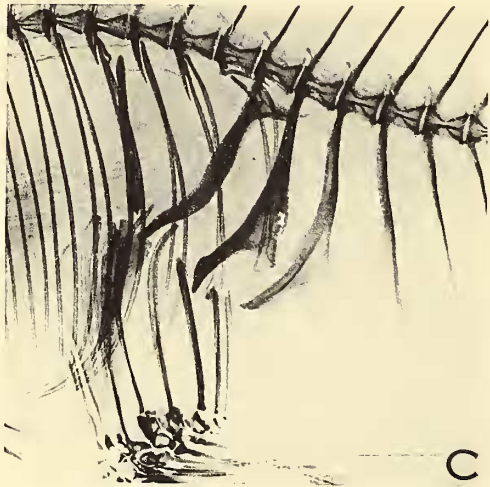
MIDDLE-AMERICAN POECILIID FISHES OF THE GENERA CARLHUBBSIA AND PHALLICHTHYS, WITH DESCRIPTIONS OF TWO NEW SPECIES



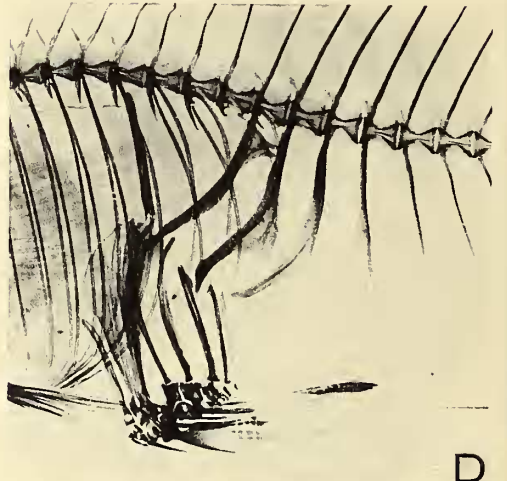
A



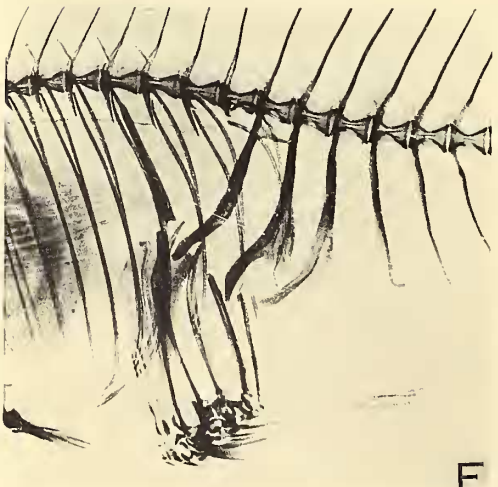
B



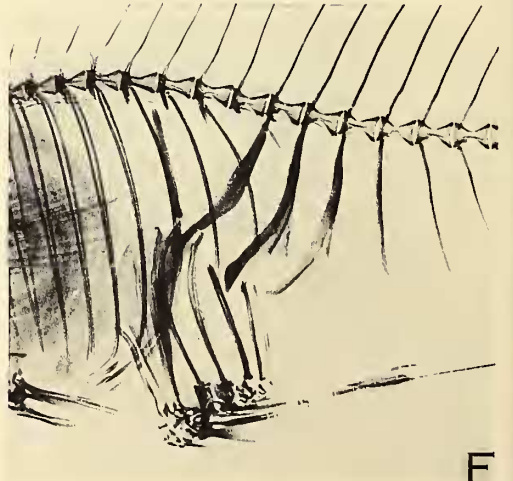
C



D



E



F

MIDDLE-AMERICAN POECILIID FISHES OF THE GENERA CARLHUBBSIA AND PHALLICHTHYS,
WITH DESCRIPTIONS OF TWO NEW SPECIES